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STERILITY IN THE STRAWBERRY

BY

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STERILITY IN THE STRAWBERRY[1]

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INTRODUCTION

This paper is a report of studies on the sex condition in strawberries (*Fragaria* spp.) which have been carried on during the past four years. The study of pistil sterility and anther abortion in the cultivated varieties and wild species, which are the result of the strong tendency of this genus toward dieciousness, has received considerable attention; but the primary object of the investigation has been to find, if possible, some satisfactory explanation for the phenomenon of pollen abortion, which is so prevalent among heterozygous plants or plants of hybrid origin.[2]

MORPHOLOGY OF THE FLOWER PARTS

INFLORESCENCE

The inflorescence of our cultivated strawberry and of *Fragaria virginiana*, which it closely resembles, is a dichasial cyme or sometimes, especially in certain cultivated varieties, a pleiochasium. The two lateral branches of the relatively main axis are not always equal either in size—that is, number of flowers borne—or in time of flowering. The pedicel of the primary flower is generally inserted a short distance from the joint of the two secondary branches and on the smaller of the two. The primary flower of the largest lateral branch usually opens directly after the primary flower and before that of the smaller lateral branch. The arrangement of the flowers and order of blooming are shown in figure 1.

Variations from these types are not uncommon. In some cases the primary flower is lacking; in others, the primary stalk seems to be made

[1] Published, with the approval of the Director, as Paper 94 of the Journal Series of the Minnesota Agricultural Experiment Station.

[2] The work was begun at the suggestion of Dr. M. J. Dorsey, of the Minnesota Agricultural Experiment Station, and I wish to express my thanks for the help and encouragement which he gave during the progress of the work. I also wish to express my appreciation of the assistance given by Dr. C. E. Allen, of the Department of Botany, University of Wisconsin, in a portion of the cytological studies and for space kindly furnished me in his laboratory during a month in 1915.

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up of two which separate at varying distances from the ground, thus producing two typical cymes from one main stalk. The peduncle and pedicel lengths vary greatly within a variety, but there is apparently a rather constant negative correlation between the two—that is, as the peduncle or primary stalk decreases in length the pedicels or secondary branches increase, resulting in a rather constant ratio between fruit stalk length and leaf petiole length or height of plant.

Opposite the point of insertion of the small secondary branch is usually a large bract. This may be and usually is in the wild forms a monophyllous leaf, while in many of the cultivated varieties it may be a well-developed di- or tri-phyllous leaf. The bracts or bracteoles subtending the branches of lesser degree are usually only rudimentary structures, being made up of the stipules often much reduced, but with an occasional slight broadening of the midvein to form a small leaf blade.

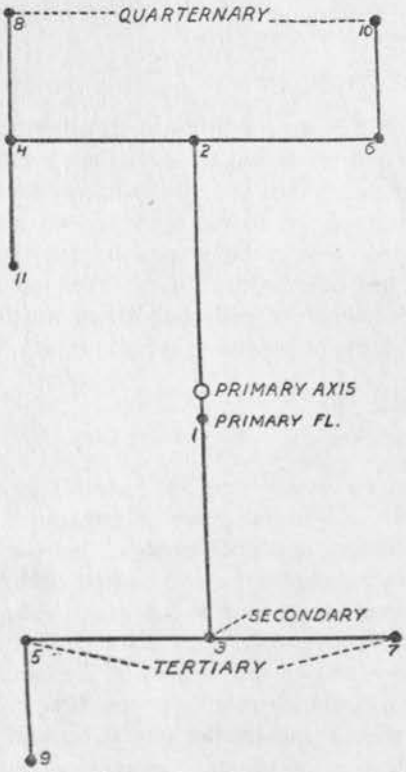

FIG. 1.—Diagram showing the arrangement of flowers of the strawberry and the order of blossoming. The approximate order of opening is indicated by the figures.

The flowers are hypogynous, and typically pentamerous with regard to all parts except the carpels. The perianth consists of three whorls of members, the outer five epicalyx lobes alternating with the five sepals and opposite to the five white petals.

STAMENS

STAMEN ARRANGEMENT.—The stamens in typical flowers are arranged in multiples of five. The number is not constant in pure species or within a variety. The stamens are arranged in three whorls. The outer consists of 10 parapetalous stamens located at either side of the base of the petals (fig. 2, *a*, *PP*). These have long filaments. Their number is the most constant of any of the whorls. The second whorl consists of five antipetalous stamens located opposite the petals and inside of the parapetalous whorl (fig. 2, *a*, *AP*). The filaments are shorter than those of the outer and inner whorls. The third whorl consists of five antisepalous stamens inserted opposite the point of insertion of the sepals, and inside of the two other whorls (fig. 2, *a*, *AS*).

Variations in stamen number from the above arrangement, if slight, are usually due to the addition or loss of one or more stamens from the antipetalous series. If a definite increase of five takes place, it may be the result of an increase in one of two places: either the 5 single antipetalous stamens may be replaced by 5 pairs to form a whorl of 10 (fig. 2, *b*, *AP*), or the 5 antisepalous stamens may have been replaced by 5 pairs of parasepalous stamens located at the same points as the whorl of 5 (fig. 2, *c*, *PS*). A further increase in the number of antipetalous stamens may consist in the development of a pair located on either side and slightly inside of the single antisepalous stamens (fig. 2, *d*, *AP*). These are characterized by the same short filament that is found in the anti-

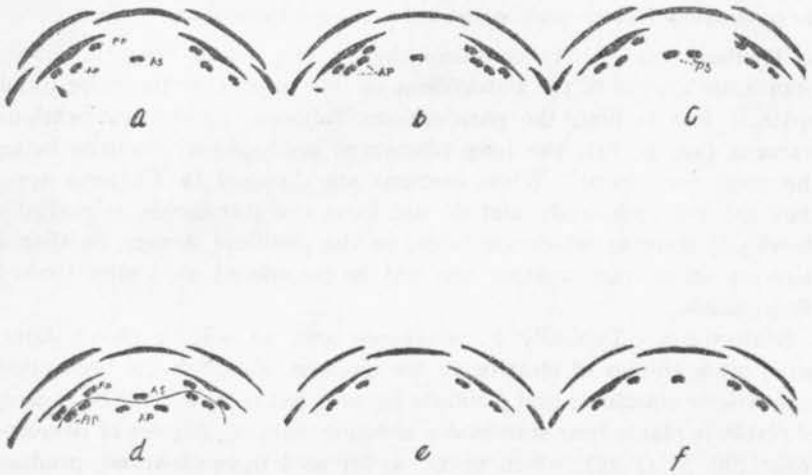

FIG. 2.—Flower diagrams of *Fragaria* spp., showing stamen arrangement: *AS* represents antisepalous; *AP*, antipetalous; *PP*, parapetalous; and *PS*, parasepalous stamens. *a* represents the 20-stamen arrangement found commonly in *F. virginiana* and *F. americana* and many cultivated varieties; *b* and *c*, a 25-stamen arrangement found in *F. virginiana* and some cultivated varieties; *d*, a 35-stamen arrangement sometimes found in cultivated varieties; while *e* and *f* represent a 10 and 15 stamen arrangement found in some clones of *F. americana*.

petalous whorl of 5. This increase, plus the 20-stamen arrangement, gives a 30-stamen arrangement, or with either of the two 25-stamen arrangements, gives 35.

Rydberg (*34*, *p. 10*)[1] has pointed out that the antipetalous stamens which appear to be the middle whorl in *Fragaria* spp. are truly an inner whorl which has been pushed out to form apparently a middle one (fig. 2, *d*), and that the outer parapetalous stamens are in reality younger with regard to development than the antisepalous or inner series. A study of the position of the accessory stamens of the antipetalous series (which can readily be distinguished by their short filament) and of the order of stamen development indicates that this view is correct.

[1] Reference is made by number (italic) to "Literature cited," p. 666-669.

In *F. americana*, 10, 15, and 20-stamen arrangements are common. The 20-stamen arrangement is the same as that described for *F. virginiana* and the cultivated varieties. When, however, a decrease below 20 to 15 takes place, it is due to the loss of the short filamented middle whorl of antipetalous stamens (fig. 2, *f*)—further proof that this is truly an inner and not a middle series. The next series to be lost is that consisting of the inner long filamented antisepalous stamens, thus leaving the parapetalous stamen arrangement (fig. 2, *e*). This seems peculiar, in view of the fact that they are older than the parapetalous stamens and therefore should remain longest. This might be considered as proof that—

the parapetalous stamens must be regarded as abnormal supernumary parts,

as Rydberg (*34, p. 11*) considers them. The genus Fragaria differs from other species of the Potentilleae in this respect, as the more usual order of loss is first, the parapetalous, followed by the antipetalous stamens (*34, p. 11*), the long filamented antisepalous stamens being the most permanent. When stamens are dropped in *Fragaria* spp., they are lost completely and do not form the staminoids or partially developed stamens which are found in the pistillate flowers, so that a decrease in stamen number can not be considered as a step toward dieciousness.

STAMINODIA.—Typically *F. virginiana* and, as will be shown later, some other species of strawberry are diecious, although the separation into strictly staminate and pistillate forms is not complete. The flowers of pistillate plants bear staminodia showing varying degrees of development (fig. 3, *11–16*), which never, as far as I have observed, produce pollen.[1] The staminate plants develop pistils which, as far as outward appearances are concerned, are normal, but which do not set fruit. As a result of this incomplete separation of the sex-bearing organs, there are variations in the stamen and pistil condition on individual clones and also on the flowers of an infloresence within a clone.

The most common condition in the staminate plants is that in which all of the flowers produce normal stamens bearing good pollen. Occasionally clones are found in which the first flower bears only staminodia in place of the normal stamens. In flowers of this type the pistils are practically always fertile and produce normal fruits. On the other hand, the primary flower may produce normal stamens and no fertile pistils while one or both of the secondary flowers may be of the pistillate

[1] A possible case of pollen production in a pistillate variety is that of the Crescent. Plants of it which I have observed are strictly pistillate, although producing very large prominent staminoids (fig. 3, *16*)—which are entirely devoid of reproductive tissue (Pl. 36, A). Castle (*7, p. 150*) states that in England "it produces perfect flowers and sets its fruit most readily, cropping heavily in favorable seasons." As most other English varieties are hermaphrodites, it is very possible that large crops might set as a result of cross-pollination, and that the presence of the extremely large staminoids has been misleading with regard to the exact sexual condition of these plants.

Fletcher (*15, p. 132*) also states that Crescent may vary in stamen condition becoming "a true staminate on rich soils," but gives no further evidence on the point.

type, in which case they set fruit. A few cases have been found in which one side of a flower produced normal stamens and sterile pistils while the other half produced staminodia and set fruit. A similar range of conditions with regard to stamens has been noticed in seedlings of certain cultivated varieties. Figures G and H, Plate 35, are from photographs of primary and secondary flowers of the seedling Minnesota 1017 × Progressive 32–1, both of which bear only staminoids, while I and J represent secondary and tertiary flowers of the same variety, I producing both staminodia and normal anthers and J producing only normal anthers. The production of pistillate flowers on the primary and on

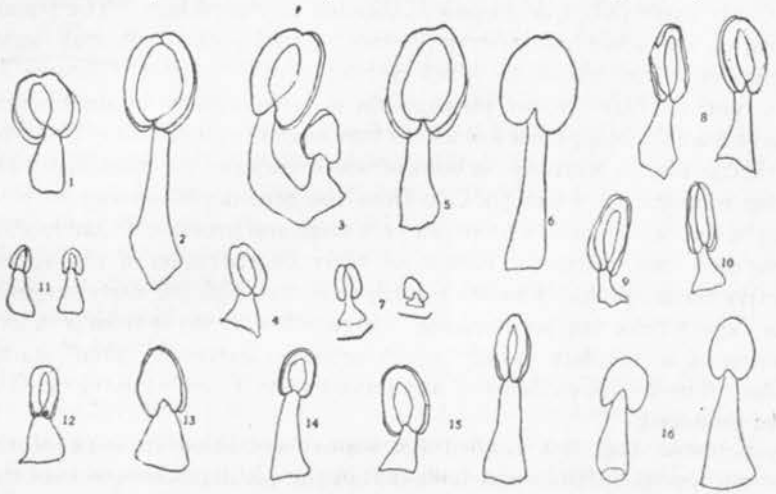

FIG. 3.—Outline camera-lucida drawings of perfect and intermediate anthers and staminodia of strawberry: *1*, *2*, and *3*, Normal anthers from tertiary flowers of a seedling of Minnesota 1017 × Progressive, Progressive, and another seedling of Minnesota 1017 × Progressive (40–1), respectively. *4*, Staminodium from a primary flower of Minnesota 1017 × Progressive (40–1). *5* and *6*, Normal anthers from Minnesota, 3 and a late primary flower of Minnesota 1017, respectively. *7*, Staminodia from a primary flower of Minnesota 1017 produced early in the spring. *8* and *9*, Intermediate anthers from primary flowers of Minnesota 3. *10*, Intermediate anther from a primary flower of Progressive. *11*, Staminodia from a pistillate flower of *F. virginiana*. *12*, *13*, and *15*, Staminodia from pistillate flowers of seedlings of Minnesota 1017 × Progressive, 2–25, 13–40, and 11–59, respectively. *14*, A staminodium from a flower of Haverland, a pistillate variety. *16*, Staminodia from a flower of Crescent, a pistillate variety which produces extremely large and prominent abortive anthers.

some of the secondary flowers throughout the season seems to be the normal condition in a number of seedlings of the cross 1017 Minnesota × Progressive (fig. 3, *3*, *4*), while among the commercial varieties there are a number which produce pistillate primary flowers early in the flowering season, while those produced later are all perfect. A few varieties which show this peculiar condition early in the spring, are Brandywine, Minnesota 3, Bederwood, Tennessee Prolific, and Staples. In figure 3, *6* represents an outline drawing of a normal anther from a primary flower of Minnesota 1017, produced late in the season, while 7 represents staminoids of the same variety taken from flowers produced early in the flowering season.

Although typically there are two rather distinct types with regard to stamen development in both cultivated and wild clones of the strawberry—namely, the perfect stamens bearing normal pollen and the staminodia of the pistillate varieties—there are apparently a series connecting these two conditions.

Figures *11*, *12*, *13*, *14*, *15*, and *16* of text figure 3 show the range of development in size of the staminodia on some pistillate plants, and *1*, *2*, *3*, *5*, and *6* show the relative size of normal anthers. In actual size the two types closely approach one another. With regard to development of reproductive tissue, there is considerable difference. The normal stamens naturally carry pollen development through to completion. The staminodia, on the other hand, never produce normal pollen, but show some variations in the extent to which development is carried. Figures A, B, C, and D, Plate 36, are photographs of cross sections of staminodia, figures A and B being cross sections of two loculi of staminodia of Crescent and Columbia, respectively, in both of which varieties the staminodia are rather prominent. Plate 36, C, is from the seedling Minnesota 1017 × Progressive, 11–59, which produces very large and prominent staminodia. Here there are distinct evidences of early degeneration of the reproductive tissue, probably pollen mother cells, although the early stages of this variety have not been studied. Figure D (Pl. 36) is from a staminodium of a pistillate variety which produces extremely small staminodia. There is no evidence of any reproductive tissue whatever having been produced.

Janczewski (*24*) has studied the stamen condition in some of the diecious species of Ribes and finds that in the pistillate flowers small stamens develop. Their internal development soon ceases and abortion of the reproductive tissue takes place. He considers that the small dark staining mass which he found in the staminodia was made up of the decomposed pollen mother cells. Often the cavity left by the breaking down of the pollen mother cells was filled with parenchyma which had grown in from the walls. Gates (*17*) found the same condition in some anthers of *Oenothera lata*. Apparently the parenchymatous tissue filling the staminodia of Crescent and Columbia is not of this origin, as early stages show no signs of the formation of pollen mother cells.

INTERMEDIATE ANTHERS.—In studying the anther types of *F. virginiana* certain clones were found which on first examination appeared to be producing normal stamens, but on closer examination were found to contain either a dark staining disintegrated mass or completely aborted microspores, the walls of which, in some cases, were disintegrating. These are apparently intermediate types between the staminodia and normal anthers. Similar types of anthers are not infrequently found in the primary flowers of many wild staminate clones.

A study of the intermediate stamens of *F. virginiana* indicates that pollen development is generally carried to the homœotypic division

or to the formation of the tetrads when degeneration occurs. This becomes apparent first through degeneration of the mother-cell wall and the cytoplasm, if the homœotypic division is taking place, leaving the spindles and chromosomes standing out sharply in this degenerate mass; or if the tetrads have already been formed, the material in which the microspores are embedded disintegrates and is followed directly by the disintegration of the microspores. Plate 36, E, shows degenerating tetrads; F shows a later stage of the same thing in which the microspores have completely degenerated; and G shows the condition found in mature anthers of this type.

Occasionally development may proceed to the formation and liberation of the microspore when, following a slight thickening of the walls, degeneration of the contents and disintegration of the microspore walls takes place. The same type of degeneration is found here as where earlier abortion takes place. The walls become thickened and, as degeneration proceeds, show a beaded appearance and finally break up into drops of a yellow oily appearing substance which makes up the mass shown in figure G (Pl. 36). In other clones of *F. virginiana* development proceeds to the liberation of the microspores from the tetrad when, following a slight development of the microspore wall, degeneration of the cell contents takes place, leaving aborted pollen of the type so characteristic of hybrids.

In the cultivated hermaphroditic varieties which produce staminodia on the early primary flowers (Pl. 36, D, G), and on some other varieties, such as Lovett, Glen Mary, and Minnesota 1017 × Progressive 9–24 (Pl. 36, B, E), these same types of anthers characterized by being small, shrunken, and bleached yellow or deep ocher are common. They show both types of degeneration—i. e., complete disintegration of the anther contents and abortion of the microspore contents following their liberation from the tetrad. Figure H, Plate 36, shows a section of a whitish yellow anther of the type shown in figure 3, *8* and *9*, from a primary flower of Minnesota 3, a variety which for the most part produces normal stamens.

Jeffrey and others have recently given emphasis to the relationship between aborted pollen and hybridity and have attempted to correlate any considerable amount of pollen abortion with a hybrid condition of the plant. Apparently in the strawberry the above type of pollen sterility and the tendency toward dieciousness are very closely related. As all degrees of stamen development may be found on a single cultivated variety of the strawberry, and on some wild plants also, from the small staminodia to well-developed stamens bearing normal pollen, it seems safe to conclude that these intermediate stamen types bearing 100 per cent aborted pollen and found in apparently pure *F. virginiana* are not the result of hybridization but are really the expression of various degrees of dieciousness.

Whether the clones of *F. virginiana* bearing these intermediate anther types are able to develop fruit, thus indicating whether they have been

derived from the pistillate forms continuing pollen development in the staminoids beyond the usual time or whether they are staminate forms in which pollen development is inhibited has not been determined experimentally. However, they appear to be of the latter type as they have been seen in flower a number of times and have shown no signs of setting fruit.

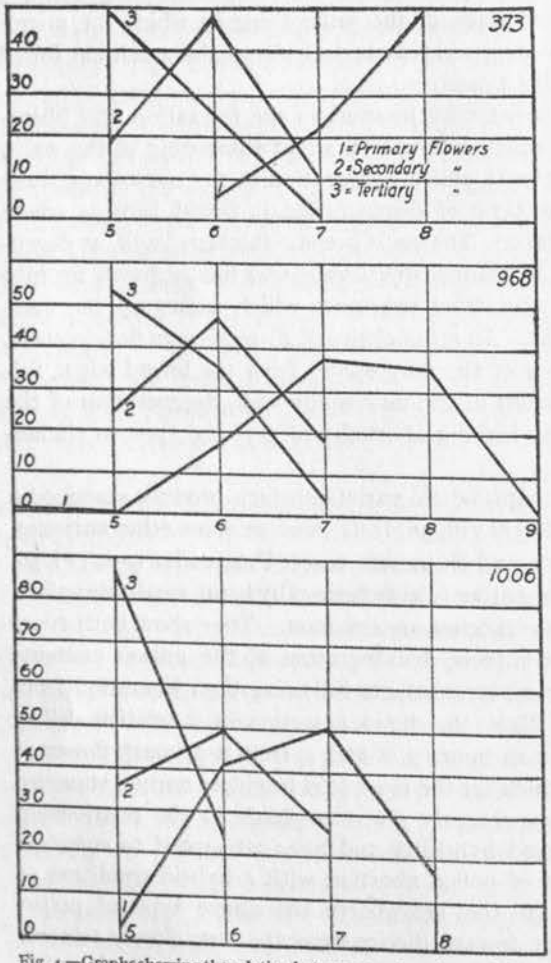

Fig. 4.—Graphs showing the relation between sepal number and flower position in the seedling varieties No. 373, 968, and 1006. The sepal number is indicated on the abscissas and the frequencies on the ordinates.

RELATION OF FLOWER PART NUMBER TO SIZE OF FRUIT

It is generally recognized by growers that toward the end of and in fact during the whole progression of the picking season of strawberries, there is a progressive decrease in the size of berries produced, but the relationship between this decrease and the position of the flowers on the inflorescence producing these smaller berries has not been so generally recognized. As has already been mentioned, strawberry flowers are typically pentamerous, but under cultivation there has been an increase in the number of parts in a portion of the flowers. This increase is most striking in the primary and secondary flowers and is only apparent to a very slight degree in the later ones. An increase in calyx-lobe number is practically always accompanied by an increase in both petal and epicalyx lobe number and as the stamens are arranged with regard to petal position there is necessarily an increase in stamen number also.

Figure 4 shows the relationship between flower position and sepal number in three seedling strawberry varieties. These show a condition typical

of our cultivated varieties. It will be seen that there is a very direct relationship between flower position and number of flower parts. In these same varieties the relationship between calyx-lobe number and size of berries was studied. The results are shown in Table I. These results indicate that there is a high correlation between flower-part number and fruit size, and as a definite relationship has been pointed out between flower position and flower-part number, it follows that the larger fruits will be developed on the early blooming primary flowers and that, as the season progresses, there will be a decrease in fruit size due to their being borne on later-blooming flowers of a higher order.

TABLE I.—*Relation of fruit size to calyx-lobe number in strawberries*

Variety.	Population.	Calyx-lobe number.			Diameter of berry.			
		Range.	Mean.	Standard deviation.	Range.	Mean.	Standard deviation.	Coefficient of correlation.
					Cm.			
Seedling 1006....	274	4–8	6.350	0.925	1.4–3.8	2.326	0.343	0.482±0.031
Seedling 373....	288	5–9	6.827	1.040	1.4–3.5	2.403	.532	.667± .022
Seedling 968....	275	5–9	6.313	.956	1.7–3.8	2.427	.4361	.519± .03

Even a casual observation of normal large and small berries of any variety will indicate that there must be a relationship between berry size and carpel number. Table II shows the direct relationship which exists between fruit position, size of fruit and achene or carpel number in all of the fruits produced on the inflorescences studied. The fact that there is such a definite relationship between size of berry and flower position should be constantly kept in mind in the selection of breeding stock. This is apparently the point that Mr. Hubach, a southern strawberry breeder, has in mind in selecting for stalks which bear only one fruit per inflorescence (*see Darrow, 9*).

TABLE II.—*Relationship between fruit position, number of achenes, and size of fruit in the strawberry*

Variety.	Primary.				Secondary.			Tertiary.			Quaternary.		
	Number of inflorescences studied.	Number of flowers.	Average number of achenes.	Average size.	Number of flowers.	Average number of achenes.	Average size.	Number of flowers.	Average number of achenes.	Average size.	Number of flowers.	Average number of achenes.	Average size.
				Mm.			*Mm.*			*Mm.*			*Mm.*
Minnesota 3.....	6	7	382.28	28.0	14	224.27	17.7	21	150.9	9.8	7	92.42	7
Wildwood.....	7	4	229.70	23.8	17	142.7	19.0	20	88.15	11.7	3	72.7	7
F. virginiana ♀	1	1	112.00	15.0	2	116.5	13.5	4	77.0	8.3	1	70.0	6

PISTILS

MORPHOLOGY.—The carpels bearing a single orthotropous ovule are arranged in a spiral on the fleshy cone-shaped receptacle. At maturity they form dry achenes either set on the surface of the receptacle, as in *F. americana*, or in shallow or deep pits, as in *F. virginiana*. The style is inserted laterally on the inner side of the carpel and extends well above the upper portion of the ovary. The pistil number is not constant on the flowers of an inflorescence but is directly dependent upon the position of the flower.

PISTIL STERILITY AND DIECIOUSNESS.—As has been previously mentioned, *F. virginiana* is, in the wild, typically diecious, the stamens having been reduced to staminodia in the pistillate plants and the pistils, although present and apparently normal, as far as can be seen superficially, in the staminate flowers are nearly always functionless. This condition of dieciousness has apparently remained unrecognized by systematists of Fragaria. Apparently dieciousness is not confined to *F. virginiana* alone, but is typical of most of the American species, except *F. americana*, which is hermaphroditic, as is also the European species *F. vesca*.

As early as 1760 dieciousness was recognized in *F. elatior* by Duchesne (*see Fletcher, 16*), who showed that the apparent sterility of the Hautboy was in reality due to the weeding out of the unproductive male plants. He also recognized partial separation of *F. chiloensis* into male and female plants. A study of herbarium material of some of the American species of Fragaria indicates that *F. chiloensis* from Alaska to Bolivia, *F. cuneifolia* on Vancouver Island and in Washington and *F. platypetala* from the north moraine of Sir Sandford Glacier are all diecious, at least some plants produced pistillate flowers bearing staminodia, while others bore flowers with well-developed stamens and apparently normal pistils which showed no signs of setting fruit. On two plants of *F. chiloensis* from Lake Merced, California, the primary flowers of staminate inflorescences were found to have set fruit, while the remaining flowers, although well beyond the fruiting stage, showed no signs of setting. Supposedly hermaphroditic plants of *F. chiloensis* from Alaska, grown at University Farm for a number of years, produced few, if any, fruits, although they blossomed profusely.

Georgeson (*19, p. 13*), in speaking of *F. chiloensis*, which he used in his hybridization experiments, says:

> There is a decided variation among the plants; some are much more productive than others, and some appear to bear only staminate flowers, though, as a rule, the flowers are perfect.

and again (*20, p. 11*):

> The flowers are large and white and many of them staminate and sterile.

The first plants of *F. chiloensis* brought to Europe by Frezier were all pistillate and had probably been selected by him because of their fruiting propensities.

Richardson (*31, p. 176*) mentioned receiving male plants of *F. virginiana* from America. I have grown plants of *F. virginiana illinoensis* from near Dresden, Ohio, which proved to be strictly diecious. The literature on strawberry growing in this country during the early part of the last century makes many references to the necessity of growing staminate varieties for the purpose of fertilizing the pistillate forms and to the fact that these plants were unproductive of fruit, but very productive of plants and would soon dominate the garden if attention was not paid to them. Apparently they were using staminate *F. virginiana* plants as pollen producers.

A study of *F. virginiana* in various sections of Minnesota shows that for the most part this species is diecious, although some few hermaphroditic plants may be found. Of a total of 1,615 pistillate flowers of this species borne on 304 plants located in four distinct regions of the State, 1,180 set fruit, while 393 were still in the bud or blossom stage, thus indicating that practically all of the flowers of the pistillate forms are fertile if pollinated. One pistillate clone, composed of 11 plants was found, however, which produced a total of 57 flowers, 18 of which were still in the bud or flower stage; of the remaining 39 only one set seed. Another clone of this same type was found in a different region. Material of both these has been saved to test further their fertility. Plants of both of these clones, when grown under conditions more favorable to pollination, proved fertile.

In contrast to the striking fertility of most of the pistillate forms is the condition in the apparently hermaphroditic plants. Of 1,640 flowers of this type borne on 381 fruiting stalks of separate plants, 403 were in the flower or bud stage, while only 152 of the remaining 1,237 set fruit, leaving a total of 1,085 flowers which were definitely sterile; 286 plants of the 381 studied bore no fruit.

The position on the inflorescence of the flowers which set is interesting in connection with the problem of nubbins and pistil sterility in our cultivated varieties. The fact has previously been mentioned that a few flowers borne on male plants may bear only staminodia in place of stamens and that these are generally fertile. Of the 152 fruits which set, 31 were developed from this type of flower. The other flowers on these stalks were of the usual staminate form and were generally sterile, although a few instances were noted in which one of the flowers bearing normal stamens set a few achenes. Of these 31 fruits, 17 were borne on primary, 10 on secondary, 3 on tertiary, and one on a quinary flower. Five of the 152 which set were borne on flowers bearing the intermediate type of anther and of these 2 were primary and 3 secondary. The other flowers of these inflorescences bore normal anthers and were sterile. Fifteen resulted from flowers which produced some staminodia and anthers either distinctly segregated in definite portions of the flower or mixed indiscriminately; of these, 12 were from primary and 3 from

secondary flowers. The remaining 101 fruits were borne on flowers bearing a full quota of normal anthers. Of these flowers 54 were primary, 40 secondary, and 7 tertiary. While most of the fruits which set on the pistillate plants were of a regular shape, indicating a perfect or nearly perfect set of achenes, those borne on the staminates were for the most part very irregular in shape, as the achenes which set were often few in number and irregularly scattered. Often not more than one or two achenes per flower developed. Where only a few achenes developed, the typical nubbins which are so common in the latter part of the picking season in commercial plantings were produced. These results prove that *F. virginiana* is a species well on its way toward dieciousness, and, reasoning from analogy with *F. virginiana* and *F. elatior*, it may be concluded that those other American species which produce two types of plants—that is, pistillate and somatic hermaphrodites—are also diecious.

Recent investigations by Bunyard (*6*) and Fletcher (*14*) into the origin of our cultivated strawberries tend to show that they have originated from hybrids of *F. virginiana* and *F. chiloensis*, both of which are apparently diecious. If this is the case, it raises the question of the origin of our cultivated hermaphroditic forms. A study of the pistil sterility in these forms seems to indicate that they may have been derived from males which have varied in regard to pistil fertility.

Table III shows the relationship between flower position and pistil sterility in 10 hermaphroditic and 4 pistillate varieties. This table was prepared regardless of the degree of setting, whether perfect or whether the resulting fruit was a nubbin, all flowers which set any achenes being put under the heading "Set." The lower horizontal row under each of the two groups indicates the percentage of the flowers of each position which set fruit. It shows the very great increase in sterility from the first flowers to the last in both the pistillate and hermaphroditic forms, being greater in the latter than the former. This is the condition which would be expected if the cultivated hermaphrodites have been derived from males of the wild type, as the males which do set fruit in the wild exhibit a high percentage of their low fertility in the primary flowers.

The conclusion that the hermaphrodites have been derived from staminate forms rather than from pistillate is in keeping with the results found in other species, as *Lychnis* spp. (*35*) and the grape (*43*). A further study of pistil sterility was made in 15 other varieties of hermaphrodites and 3 pistillates to determine the relationship between nubbins or irregularly set fruit and flower position.

Nubbins and lack of setting of flowers have been attributed by horticulturists for the most part to lack of proper pollination or to frost injury. The first of these factors may be eliminated, however, as pollen is usually very plentiful and in a mixed planting, such as the data given in Tables III and IV were taken from, was always abundant and especially so when

the later more sterile flowers were in blossom. Further, the fact that pistillate varieties, grown in proximity to hermaphrodites, set fruit even in the early part of the season, when pollen is admittedly scarce, would argue for pollination having little to do with nubbin formation. To those who have noticed the effect of frost on strawberry flowers it will be clear that this factor may also be eliminated as a cause of irregularly set fruit, as frost, if it injures the flower at all, will blacken the entire receptacle. The possibilities of the primary flowers being "frostbitten" are much greater than the later ones, but it is the latter which generally form nubbins or are entirely sterile.

TABLE III.—*Relationship between flower position and number of fruits set in hermaphroditic and pistillate varieties of strawberries*

Variety.	Sex.	Number of stalks.	Primary.		Secondary.		Tertiary.		Quaternary.		Quinary.	
			Set.	Not set.	Set.	Not set.	Set.	Not set.	Set.	Not set.	Set.	Not set.
Reasoners 324	☿	40	44	.....	85	6	87	40	7	29	.....	.....
Seedling 947	☿	40	39	4	66	22	55	50	3	4	.....	.....
Orem	☿	40	48	.....	111	11	68	45	5	7	.....	.....
Lovett	☿	40	42	.....	79	3	77	28	7	13	.....	.....
Seedling 893	☿	40	42	.....	72	10	58	58	4	39	.....	.....
Seedling 1023	☿	40	43	.....	83	5	90	33	18	16	.....	2
Abington	☿	40	49	2	77	8	82	18	19	19	1	2
Everbearing	☿	40	41	.....	90	.....	107	15	16	17	.....	1
Glen Mary	☿	40	52	.....	63	19	20	44	.....	8	.....	.....
Seedling 924	☿	40	52	.....	74	23	41	25	2	3	.....	.....
Total	.....	.....	452	6	800	107	685	356	81	155	1	5
Per cent	.....	.....	98.7	1.3	88.2	11.8	65.8	34.2	34.3	65.7	16.6	83.3
Paul Jones	♀	40	48	.....	84	9	37	39	10	.....	.....	.....
Marie	♀	40	49	.....	75	12	84	12	10	22	.....	.....
July	♀	40	50	.....	111	6	48	37	70	55	.....	6
Wildwood	♀	8	11	.....	16	2	8	1	.....	3	.....	.....
Total	.....	.....	158	.....	286	29	177	89	90	80	.....	6
Per cent	.....	.....	100	.....	90.8	9.2	66.5	33.5	52.9	47.1	.....	100

Table IV shows the relation between flower position, imperfectly developed fruit or nubbins, and complete pistil sterility. It corroborates what has already been pointed out, namely, that the first flowers of an inflorescence are much more fertile than the later ones. With regard to nubbins the same relationship is shown—that is, there is a gradual increase in the percentage of nubbins formed from the primary to the last flowers which open. This condition can hardly be construed as indicating anything but a morphological sterility of a portion of the pistils in those flowers which result in nubbins, if viewed with the facts in mind of the condition shown in the hermaphrodites of the wild parent species, the unquestionable sterility of many of the later flowers, and the fact that the greater percentage of these partially sterile flowers are in bloom when pollen is most abundant. If it were a question of pollination, we would expect the pistillate forms to exhibit much more sterility than the hermaphrodites, whereas they exhibit decidedly less, both with regard to the actual number of sterile flowers as well as nubbins.

TABLE IV.—*Relationship between flower position and the degree of setting in hermaphroditic and pistillate varieties of strawberries*

Variety.	Sex.	Number of stalks.	Primary.			Secondary.			Tertiary.			Quaternary.			Quinary.		
			Perfect.	Nubbins.	Not set.	Perfect.	Nubbins.	Not set.	Perfect.	Nubbins.	Not set.	Perfect.	Nubbins.	Not set.	Perfect.	Nubbins.	Not set.
Dorman	♀	20	17	2	1	53	13	2	43	23	45	8	11	55	....	....	....
Haverland[a]	♀	20	17	2	1	42	11	....	74	23	1	32	11	6	....	....	....
Parson's Beauty	♀	20	21	0	0	84	7	3	62	24	35	13	15	39	....	....	....
Bederwood	♀	20	15	5	0	36	16	....	74	28	....	28	14	5	....	....	....
Steven's Late Champion	♀	24	36	18	5	27	40	46	3	9	30	....	....	....	....	....	....
Helen Davies	♀	20	19	1	....	60	12	3	74	51	12	31	10	27	....	....	....
Senator Dunlap	♀	20	21	1	....	45	16	....	35	19	48	9	11	44	....	....	....
Pride of Delaware	♀	20	18	5	....	47	23	4	33	47	33	16	16	36	....	....	....
Minnesota 3	♀	20	22	....	....	64	2	....	70	25	6	26	16	10	....	....	....
Seedling 924	♀	20	37	....	....	73	4	....	63	2	7	1	....	....	....	....	....
Seedling 937	♀	20	30	....	....	68	4	....	95	6	9	24	8	....	....	....	....
Seedling 947	♀	20	26	1	....	39	9	....	59	4	7	11	1	14	....	....	....
Seedling 876	♀	20	27	....	....	73	....	....	85	1	2	7	1	8	....	....	....
Seedling (number lost)	♀	20	25	....	....	64	5	1	72	17	21	6	4	7	....	....	....
Seedling 778	♀	20	24	....	....	67	2	....	88	5	....	29	1	....	....	....	....
Total	....	....	355	35	7	842	164	59	930	284	256	241	119	251	....	....	....
Per cent	....	....	89.4	8.8	1.8	79.1	15.4	5.5	63.3	19.3	17.4	39.4	19.5	41.1	....	....	....
Enormous	☿	20	19	0	....	62	16	....	95	44	4	46	19	23	....	....	2
Warfield	☿	20	15	4	....	46	8	....	52	27	2	24	10	10	....	....	....
Crescent	☿	20	20	....	....	56	10	....	90	21	6	57	10	6	2	1	....
Total	....	....	54	4	....	164	34	....	237	92	12	127	39	39	2	1	2
Per cent	....	....	93.1	6.9	....	82.8	17.2	....	69.5	27	3.5	62	19	19	40	20	40

[a] Not certainly true to name.

The most characteristic type of nubbin is that in which all of the achenes set except those situated at the tip, thus producing a berry with a dead, dry tip. This raises the question as to why the tip pistil should be more sterile than those at the base.

We have already seen that when a reduction in stamen number takes place it is the youngest which are lost first, and apparently this is true also of the pistils. The pistils of the oldest flowers are decidedly more fertile than those of the later flowers, and it seems logical that the older pistils within a flower should be the more fertile. Observations on a seedling everbearing variety which in the spring produced only stamens and a small, white dome destitute of pistils in place of the ordinary receptacle, but which later in the season gradually produced normal flowers, illustrates this point. It was noticed that the first flowers which produced pistils developed only a few normal ones around the base of the receptacle, while those above gradually decreased in size until at the tip there were none. The later fruiting stalks increased the number of normal pistils until in the last fruiting stalks the entire receptacles of the first flowers were covered with normal pistils. This series of flowers, although an extreme with regard to sterility, still indicates the portion of a flower in which there is the greatest likelihood of its appearance. The question of pistil sterility should be kept in mind in the selection of breeding stock, as it is most certainly inherited in the pure species and apparently is in the cultivated varieties, as selfed seed of Glenville, a variety which rarely sets more than an occasional primary flower,

produced a number of seedlings which were as sterile as the parent. (All the progeny have not yet flowered.)

Sufficient pistillate varieties have not been studied to indicate definitely whether there is always a distinct difference between the ability of these and of the hermaphrodites to set fruit on the later flowers; however, a comparison of the percentage of fruit set on the tertiary and quarternary flowers of the pistillate and staminate varieties reported in Tables III and IV would seem to indicate that the former are decidedly more fertile than the latter, as is also the case in the wild forms. Darrow (*9*) reports that Mr. Hubach will use only pistillate varieties as the female parents because of the decrease in fruit production when hermaphrodites are used as both parents.

A cytological comparison of the sterile pistils of wild males and the sterile pistils of hermaphrodites may give further evidence as to the origin of sterility in the varieties which produce many nubbins and entirely sterile flowers. Strasburger (*39*) has shown that in a male resulting from a cross between *F. virginiana* ♀ and *F. elatior* ♂, the pistils which are apparently ready for fertilization already, in longisection, show a mass of degenerating material which contains the embryo sac mother cell. This may or may not be the condition in the pure forms of these species and in the sterile pistils of cultivated varieties.

To the commercial grower of strawberries as well as to the breeder the question of variation of fertility under varying conditions of environment or culture is of importance. Evidence which indicates that fertility is affected somewhat by environmental or seasonal conditions is given by the seedling which in the spring produced strictly male flowers but which in the summer and early autumn produced fertile pistils as well as stamens. Further, it is a matter of common observation that a bed of berries, if allowed to fruit more than one year, will produce an increasing number of small berries and nubbins. Of actual observational evidence the following indicates that growth conditions have something to do with sterility: A variety, named "Glenville" for convenience, was sent to the Station with inquiries as to why it did not set fruit. Plants of it were grown in the greenhouse during the late winter, and, although they produced numerous fruiting stalks and an average of 13 flowers per stalk, only an occasional primary or secondary flower set fruit. Some of these plants, after having been grown in benches, were put into pots and given little attention. On June 5 they were fruiting, and a count was made of the flowers which had set. On 6 fruiting stalks there was a total of 43 flowers, an average of slightly over 7 per stalk. Of these, 22 set fruit. Of 6 primaries there was 1 which set, of 12 secondaries 10, of 19 tertiaries 11, and of 6 quaternaries none set. The previous year some plants of this variety had been planted in the field; and 20 days after taking the above notes, observations were made on the field plants. Of 105 fruiting stalks examined, bearing a total of 1,292 flowers, an average of 12.3 flowers per stalk, there was a total of

20 fruits, of which 15 were borne on primary flowers, 4 on secondaries, and 1 on a tertiary. Although this variety shows an extreme case of sterility, the condition found as regards variability of sterility may be an indication of what will be found when a thorough study is made of this point in our cultivated varieties.

Thus far the study of sterility has dealt mainly with those types of sterility induced by a decided tendency toward dieciousness in species of *Fragaria*. Another type of sterility very prevalent in cultivated varieties and undoubtedly a factor in pollination is expressed in the appearance in ripe pollen of varying amounts of defective grains. It is with this type of sterility that the remainder of this paper deals.

POLLEN DEVELOPMENT AND STERILITY

A careful cytological examination of the pollen condition in the strawberries, both wild and cultivated, was made with the objects of determining (1) the amount of viable pollen in cultivated varieties and its relation to the setting of fruit and (2) the cause of pollen abortion in plants of hybrid origin.

The material used as a basis in determining the general pollen condition in *Fragaria* spp., consisted of (a) *F. virginiana* from various parts of Minnesota, (b) *F. americana*, (c) a considerable number of cultivated varieties, and (d) seedlings under test in the course of the fruit-breeding work. The cytological study was carried on principally on the self-fertile variety Minnesota No. 3, a cross of Senator Dunlap × Pocomoke, recently introduced by the Minnesota Agricultural Experiment Station. It produces, on an average, about 50 per cent of aborted grains and so furnishes desirable material for the study of normal and abnormal pollen development. The stages in normal development were also studied in *F. virginiana*.

POLLEN CONDITION IN WILD FORMS

The recent work of Jeffry and his students on the pollen condition in wild forms puts under suspicion the genetic purity of the Rosaceae in general. The forms which have been studied most intensively, Onagraceae (*25*), *Crataegus* spp. (*37*), *Rubus* spp. (*23*), and *Rosa* spp. (*8*), show, in some species, a relatively large proportion of aborted pollen and the appearance of many subspecies, some of which appear to be hybrids. Because of this fact and with a view to comparing the pollen condition of the wild with the cultivated forms, pollen of *F. virginiana* and *F. americana* was examined.

The methods used in determining the amount of abortive pollen were as follows: Fresh flowers were collected and either were allowed to dry or were kept with their pedicels immersed in water until the anthers had dehisced. The pollen was then transferred to slides by holding the flower over a slide and giving it a few sharp taps. In this way the anthers dehisced completely onto the slide. A drop of lactic acid was then added, and a small cover slide placed over the drop, forming a

fairly permanent mount if handled carefully. The lactic acid has the advantage over water or alcohol for this purpose, as it is not volatile and seldom, if ever, breaks the pollen grains through osmotic pressure. It readily enters and expands the normal grains, while it leaves the aborted ones collapsed. It has another very distinct advantage over the more mobile liquids, in that its viscosity holds both the normal and aborted grains in place until the cover has settled firmly, while, if water is used, the empty grains have a decided tendency to wander toward the edge of the cover slide, thus invalidating the count. Where no aborted pollen was present, of course no actual counts were made; but where present, counts were made varying from 200 to 2,000, the object in each case being to include enough grains to indicate within a close range the percentage of abortion. A record was kept of the position on the inflorescence of the flower from which the pollen was collected in order to determine whether a similar relationship existed between flower position and abortion of pollen as was found to exist between flower position and stamen type in certain clones.

The results of the pollen counts on 223 flowers of *F. virginiana* are shown in Table V. They indicate that *F. virginiana* produces for the most part morphologically perfect pollen, although a few plants were found in which the percentage of aborted grains was high. If pollen condition may be taken as a criterion of species' purity it may be said that *F. virginiana* in this region is nearly a pure form. The appearance of considerable amounts of aborted pollen in a few plants might be considered as the results of the "conditions" under which these plants have been grown, but the fact that several flower types have been found in the wild may indicate that abortion is due to a condition arising from a slight degree of hybridity consequent on the intercrossing of these forms. The one primary flower which produces 100 per cent aborted pollen bore intermediate anthers and abortion was more likely due to the partial suppression of stamens, in some way connected with the tendency toward dieciousness, than to other causes which may result in sterility. This was not included in the average percentage of aborted pollen in the primary flowers for this reason.

A comparison of the pollen condition in the flowers borne on various positions shows that pollen abortion is in no way related to flower position and thus to dieciousness as are the various anther types and sterile pistils before mentioned.

In the hermaphroditic species *F. americana* nearly the same condition exists with regard to the degree of perfection of pollen as in *F. virginiana*. The result of pollen counts on 49 flowers taken from an equal number of plants are shown in Table VI and they indicate that the pollen condition of *F. americana* is normal. As it is very difficult to cross *F. virginiana* and *F. americana*, it is probable that where these two species are growing in close proximity they remain pure.

TABLE V.—*Pollen condition in wild plants of Fragaria virginiana with reference to the position of the flower on the inflorescence*

Aborted percentage.	Number of primary flowers.	Number of secondary flowers.	Number of tertiary flowers.	Number of quaternary flowers.	Number of flowers position not recorded.
0	9	11	5	.....	1
1	15	18	6	.....	14
2	16	5	4	.....	11
3	6	5	.....	.....	6
4	4	3	1	.....	5
5	5	2	1	.....	3
6	1	3	.....	.....	7
7	1	4	.....	.....	2
8	0	2	2	.....	1
9	1	2	.....	.....	.....
10	3	1	.....	.....	3
11–15	4	1	3	.....	6
16–20	2	1	.....	1	4
21–25	2	.....	1	.....	2
26–30	1	.....	.....	.....	2
31–35	1	.....	.....	.....	1
36–40	.....	.....	.....	1	.....
100	[a] 1	.....	.....	.....	.....
Total	72	58	23	2	68
Average percentage of abortion	4.9	3.2	4.3	[b] 28.0	6.9

[a] Not included in average because borne in an intermediate type of anther.
[b] Of no significance because of few flowers.

TABLE VI.—*Pollen condition in wild plants of F. americana with reference to the position of the flower on the inflorescence*

Aborted percentage.	Number of primary flowers.	Number of secondary flowers.	Number of flowers position not recorded.
0	.....	.....	6
1	1	4	3
2	7	4	2
3	2	.....	3
4	3	.....	.....
5	.....	.....	1
6	1	1	1
7	.....	1	.....
8	.....	1	1
9	.....	.....	.....
10	.....	.....	2
11	.....	1	.....
12	.....	.....	2
13	.....	1	.....
14	.....	.....	1
15	.....	.....	.....
Total	14	13	22
Average percentage of abortion	2.8	4.4	5.2

Observations on the pollen condition in herbarium material of other species than those above mentioned are not conclusive with regard to the species examined because of the scarcity of material. Plants of *F. chiloensis* from Sequin, Washington, from two localities in San Francisco County, California, and from Bolivia, South America, produced perfect pollen. A single plant from Vark Hill, Cal., produced small amounts of defective grains while two plants of a clone from Lake Merced, Cal., which set fruit on the primary flowers of an otherwise staminate cluster, produced in the neighborhood of 50 per cent of aborted grains. A plant of *F. chiloensis* var. Scouleri, from Klantaak Island, Yakutat Bay, Alaska, produced perfect pollen. *F. platypetala* from Mt. Carleton, Wash., also produced perfect pollen. Although flowers of comparatively few plants of these two species have been examined, the facts seem to indicate that the pollen condition is much the same as that found in *F. virginiana* and *F. americana*.

POLLEN CONDITION IN CULTIVATED FORMS

In contrast to the nearly normal pollen condition of the wild species is the variable condition found in the cultivated forms in which practically all have a larger or smaller percentage of aborted grains. The pollen conditions in varieties, controlled seedlings of varieties, and some species-variety hybrids are given in Table VII. The percentages given are based on an average of over 600 grains per count, and indicate fairly accurately the pollen condition of the flowers studied.

TABLE VII.—*Percentage of aborted pollen in flowers, of various positions, from 120 cultivated varieties, 18 controlled seedlings of cultivated varieties, 33 selfed seedlings of one of these, 3 F_1 plants of F. chiloensis × Wilson, 7 F_1 plants of F. cuneifolia × Magoon, and 10 F_2 plants of F. vesca × F. cuneifolia. The percentages are based on an average of over 600 grains per count*

Variety.	Position of flower.			
	Primary.	Secondary.	Tertiary.	Position not recorded.
Cultivated:				
Abington		37.0	7.0	
		20.0	19.8	
Abundance	26.5	10.5	2.0	
		33.0	2.8	
Amanda	34.2		10.0	16.3
				7.7
				9.1
Arizona	63.0	70.9		
Aroma	1.5		22.4	
Barrymore	13.6	4.8	9.7	
Beacon		1.0		
Bederwood	90.8	97.0	99.3	31.7
			88.7	94.3
		92.0		100.0
Bradley			71.4	
Brandywine	21.0		14.1	12.5
				5.9
Brown Beauty		10.5	9.7	
Charles		39.0	36.7	
Chesapeake		47.0		

TABLE VII.—*Percentage of aborted pollen in flowers, of various positions, from 120 cultivated varieties, 18 controlled seedlings of cultivated varieties, 33 selfed seedlings of one of these, 3 F_1 plants of F. chiloensis × Wilson, 7 F_1 plants of F. cuneifolia × Magoon, and 10 F_2 plants of F. vesca × F. cuneifolia*—Continued

Variety.	Position of flower.			
	Primary.	Secondary.	Tertiary.	Position not recorded.
Cultivated—Continued:				
Clara			1.8	
Climax		42.5	24.8	
Clyde	45.5		61.4	38.2
Commonwealth		2.0		
Cooper			32.3	
Corsican	13.0		9.4	10.5
Darlington		27.0	11.2	
Deacon		56.0		
Dewdrop		1.8		
	38.5			
Dorman			7.7	10.3 39.6 38.5
Duncan				
Early Giant		2.0	16.6	
Early Jersey Giant	23.2		35.6	
Early Ozark	38.0		6.0	
Ekey	50.0		42.3	
	1.5	0.0	10.6	
	0.0			
Enhance	7.9		87.4	
Everbearing		79.6		
Ewell's Early		61.5	10.8	
Excelsior	66.0		1.3	
Fendell		12.0		
First Quality	54.0		68.4	
Frances E. Willard	4.9		34.2	
Fitting Eclipse			5.2	
Gandy	66.8	87.4	61.0	
		59.1		
Gill	68.8		48.0	
				51.5 44.9
Glen Mary	63.7		46.7	100.0 97.3 100.0 98.0
Glenville				17.6
Gold Dollar				
Gold	63.1			
Good Luck			50.0	
Goree	56.0	31.0		
Grand Marie	53.0		44.0	
Hanbeck Beauty	1.0		42.9	
Haverland [a]	69.9		42.9	
Ideal	27.1		36.5	
	63.0		56.0	3.0 67.8
Indiana	39.7		43.5	
Jas. Todd	20.5		15.8	
Jerome	82.3		69.6	
				51.0
Jessie	8.6			14.3
Jewell Improved	6.5		50.0	
Jewell	9.5			
Jocunda			38.5	
Joe	39.5		72.4	
Kevitt Wonder	60.0		33.1	
King Edward	80.8			
Klondike	33.8		12.6	
	73.7		50.1	
Late Jersey Giant	54.0	84.3		53.7 11.8
	6.8		13.0	15.0
Lea	2.7	5.6	6.8	
	86.6	70.2		
Longfellow	44.9	46.5		
	97.7		54.7	
	46.0	19.1	43.5	
Lovett	99.0			100.0 100.0
	84.3			95.0
				92.5
	76.9	83.9	86.9	85.8 84.0

[a] Not certainly true to name.

TABLE VII.—*Percentage of aborted pollen in flowers, of various positions, from 120 cultivated varieties, 18 controlled seedlings of cultivated varieties, 33 selfed seedlings of one of these, 3 F_1 plants of F. chiloensis × Wilson, 7 F_1 plants of F. cuneifolia × Magoon, and 10 F_2 plants of F. vesca × F. cuneifolia*—Continued

Variety.	Position of flower.			
	Primary.	Secondary.	Tertiary.	Position not recorded.
Cultivated—Continued:				
Magoon	.....	31.9	.....	.....
Malinda	11.3	.....	8.6	.....
Manhattan	32.6	.....	50.8	.....
	44.5	.....	.....	.....
	44.1	.....	.....	.....
Marshall	6.0	.....	.....	24.8 15.5 33.3 25.0 25.0
Mascot	82.0	.....	43.5	.....
Michell Early	65.6	.....	21.7	.....
Miller	97.5	.....	18.9	.....
Minnesota 3	28.7	52.1	47.1	.....
	41.9	60.4	41.8	.....
	47.5	14.2	41.9	.....
			39.5	.....
Missionary	86.8	.....	57.5	.....
	45.3	38.0	81.4	.....
Model	1.5	.....	4.0	.....
New Home	47.4	.....	67.2	.....
			50.5	.....
New York	3.5	.....	1.0	.....
Nick Ohmer	.....	.....	15.0	38.4 81.1
Ohio Boy	17.2	.....	45.5	93.0 73.0
Orem	94.2	.....	25.0	.....
Oswego	10.2	.....	19.8	.....
Palmer	96.3	.....	72.5	.....
Panama	.....	.....	11.5	.....
Pan American	21.7	.....	10.3	.....
Park Beauty	.....	.....	29.6	.....
Parson's Beauty	.....	.....	22.0	60.0
Pearl	.....	.....	53.8	.....
			43.5	.....
Pennell	44.4	.....	39.9	50.0 56.1 9.0 18.0 16.9 15.4 49.8
Pineapple	20.0	.....	16.2	.....
Pitcher Eclipse	.....	.....	.....	63.8
Progressive	75.3	.....	41.8	28.1 14.5
Prolific	26.7	.....	42.9	.....
			7.8	.....
Pride of Delaware	.....	.....	.....	62.0
Providence	24.0	26.4	23.3	100.0
Purcell Early	.....	.....	.....	100.0
Purcell	.....	.....	55.7	.....
Reasoner 324	.....	.....	53.5	.....
Rewatisco	.....	.....	91.5	35.6 37.4 40.0
Ridgeway	.....	.....	23.1	45.4 82.6 44.3
Sample	29.6	.....	19.2	31.3 60.5 29.6
Saratoga	.....	.....	61.7	.....
Saunders	.....	.....	46.7	.....
Seedling 373	62.0	.....	30.7	84.4 85.9
Seedling 585	7.0	.....	0.5	.....
Seedling 702	85.1	.....	24.1	.....
Seedling 753	54.0	.....	3.0	.....
Seedling 776	12.5	3.5	3.9	.....
			6.0	.....

TABLE VII.—*Percentage of aborted pollen in flowers, of various positions, from 120 cultivated varieties, 18 controlled seedlings of cultivated varieties, 33 selfed seedlings of one of these, 3 F_1 plants of F. chiloenis × Wilson, 7 F_1 plants of F. cuneifolia × Magoon, and 10 F_2 plants of F. vesca × F. cuneifolia*—Continued

Variety.	Position of flower.			
	Primary.	Secondary.	Tertiary.	Position not recorded.
Cultivated—Continued:				
Seedling 778	24.8	.....	20.0	25.5, 14.2, 9.9
Seedling 813	.....	.....	77.5	58.0
Seedling 825	79.8	.....	54.1	.....
Seedling 893	.....	.....	61.8	65.0
Seedling 908	.....	.....	29.6	17.5, 5.0, 11.3
Seedling 923	9.0, 13.0	.....	.....	.....
Seedling 924	.....	.....	15.2	.....
Seedling 927	.....	.....	31.0	.....
Seedling 947	.....	.....	10.0	.....
Seedling 1010	.....	.....	59.3	96.0, 55.4
Seedling 1017	.....	.....	14.3	.....
Seedling 1043	.....	.....	2.2	20.5, 24.5, 2.7, 2.0
Seedling 1045	.....	.....	.....	8.9
Senator Dunlap	.....	.....	13.8	.....
Son's Prolific	.....	.....	45.9	36.6, 20.0, 29.4
South Dakota	18.5	25.4	.....	.....
Splendid	.....	15.9	20.0, 34.9	36.7, 50.9, 58.4
Splendid × Dunlap	100.0	99.9	99.9, 98.8	100.0
Staples	.....	.....	46.3, 28.6	37.5, 51.9, 51.0
Steven's Late Champion	.....	.....	.....	24.8, 63.6, 70.6, 50.6
St. Louis	.....	.....	57.9	.....
Success	.....	.....	1.0	.....
Sweetheart	.....	.....	52.1, 69.0	.....
Tennessee Prolific	52.5	55.4	75.8	.....
Texas	.....	.....	40.0, 45.2	.....
Three Ws	.....	25.0	4.6	.....
Twilley	.....	.....	2.2	.....
Uncle Jim	.....	.....	10.2	.....
Warren	.....	.....	80.6	.....
Warfield [a]	.....	.....	9.5	.....
Wm. Belt	.....	.....	1.6	.....
Wilson	.....	.....	.....	.....
Winner	.....	43.3	1.2	.....
Wolverton	.....	.....	55.4	.....
Wonder	.....	.....	7.8	.....
Average	43.2	38.3	34.2	45.9
Selfed seedlings of Seedling 778:				
24–3	.....	47.1	.....	.....
24–4	77.2	52.4	.....	.....
25–1	.....	27.9	.....	.....
25–2	77.0	.....	17.0	.....
25–3	17.0	6.0	.....	.....
25–6	49.2	.....	.....	.....
26–1	.....	9.5	.....	.....
26–4	.....	.....	.....	43.6
27–5	52.3	.....	52.2	.....
28–3	24.5	.....	.....	.....
53–4	23.5	.....	.....	.....
54–2	21.1	.....	.....	.....

[a] Not certainly true to name.

TABLE VII.—*Percentage of aborted pollen in flowers, of various positions, from 120 cultivated varieties, 18 controlled seedlings of cultivated varieties, 33 selfed seedlings of one of these, 3 F_1 plants of F. chiloensis × Wilson, 7 F_1 plants of F. cuneifolia × Magoon, and 10 F_2 plants of F. vesca × F. cuneifolia*—Continued

Variety.	Position of flower.			
	Primary.	Secondary.	Tertiary.	Position not recorded.
Selfed seedlings of Seedling 778—Continued:				
56–4			25.3	
65–2		9.9		
65–3		22.5		
		19.4		
65–4		52.4		
		42.5		
66–1				32.0
66–2	94.2	99.0		
66–3		43.9		
67–1	25.8	38.1		
67–3			41.3	
67–4	99.0			
67–5	9.1	10.6		
		22.2		
71–5		21.3		
71–7	46.0			
72–1	100.0	33.1		
72–2			25.9	
72–3	0.4			
72–4	49.1	50.8	34.9	
72–6		52.7		
73–3			1.8	
73–4			62.8	
73–5	34.7	61.0		
Average	47.1	36.1	32.7	37.5
3 F_1 plants of *F. chiloensis* × Wilson:				
1			95.0	
2			77.1	
3		58.0		
Average				76.7
7 F_1 plants of *F. cuneifolia* × Magoon:				
1			5.2	
2	15.0			
3	2.0			
4	21.4			
5		18.2		
6	16.4			
7		29.1		
Average				15.3
10 F_2 plants of *F. vesca* × *F. cuneifolia:*				
1	11.2			
2	7.7			
3	8.3			
4	8.0			
5		19.3		
6	7.3			
7		7.0		
8	11.9			
9		5.2		
10			3.1	
Average				8.9

The most striking fact exhibited by the counts in Table VII, other than the general presence of some aborted pollen, is the variability of the pollen condition within a variety. Abington, for instance, shows a range of from 7 to 37 per cent of abortive pollen. Abundance from 2 to 33 per cent, and Bederwood, which usually produces a high per-

centage, in one instance produced as low as 31.7 per cent of abortive grains. Numerous other equally striking variations in pollen abortion will be evident by referring to the table.

In view of the variability shown above, the pollen condition was determined in all of the flowers from two inflorescences of Minnesota 3 to determine what variations occur in flowers grown under so nearly similar conditions. The results of these counts are presented in Table VIII and exhibit as great variability within the flowers of a cluster as is found between flowers from separate plants. In one stalk the range is from 31.2 to 91.1 per cent, in the other it is from 21.4 to 40.3 per cent, while the range in other counts of the same variety (Table VII) from different plants is from 14.2 to 60.4 per cent.

TABLE VIII.—*Percentage of aborted pollen in all of the flowers from two stalks of Minnesota 3*

Stalk.	Primary.	Secondary.	Tertiary.	Quaternary.
Stalk I	40.3	29.9	21.4	.....
		30.6	.....	.....
Stalk II	(a)	91.1	42.3	42.6
		63.5	68.2	42.7
		70.7	31.2	.....
		78.9	49.7	.....

[a] Anthers intermediate.

In view of the variability shown between different plants of the same variety and between different flowers of a single inflorescence, a study was made of the variation in pollen conditions of individual anthers within a single flower. The pollen of nine anthers, from a flower of Seedling 778 was studied, four of which were from the outer parapetalous series, three from the middle antipetalous series, and two from the inner long filamented antisepalous series. The results, given in Table IX, show a greater range of variability between the anthers of a single flower than was exhibited by the five separate flowers of the same variety reported in Table VII. Because of the extremely great variability in pollen condition shown by some varieties, as Abington, Abundance, Aroma, Darlington and others, which often produce nearly perfect pollen (as far as can be determined by this method of study), while at other times, apparently under the same conditions, high percentages of abortive pollen are produced, too much stress should not be laid on a few scattered observations in determining whether a species is pure or of hybrid origin until more is known of the factors which produce such great variability. It may, of course, be argued, and logically, that a large number of the grains in the anthers, which produce nearly perfect pollen, are truly abortive, but have developed beyond the stage where

degeneration can be discovered by a superficial examination. The possibility of this being the case will be shown later. Nevertheless the factors causing a relatively high degree of pollen abortion in apparently pure species have been so little studied that to assign hybridity as the only cause is, to say the least, presumptive.

TABLE IX.—*Variation in percentage of pollen abortion in anthers from one flower of Seedling 778*

Stamen position.		
Parapetalous.	Antipetalous.	Antisepalous.
29.18	33.65	27.27
50.00	38.65	41.87
41.70	17.09	.....
34.61	.....	.....

POLLEN GERMINATION TESTS

In view of the possibility of many of the apparently normal grains being in reality abortive, attempts were made to determine the exact amount of fertile pollen without regard to its apparent morphological condition. The usual method of pollen germination in Van Tieghem cells was employed. The results were disappointing, so far as a determination of actual condition of individual grains was concerned; but nevertheless some suggestive conclusions may be drawn from them. In all, 450 tests were made, comprising 28 of *F. americana*, 45 of *F. virginiana*, and 377 of cultivated varieties. The results obtained under carefully controlled conditions were very erratic. Solutions of cane sugar in distilled water were used in concentrations varying from 7 to 60 per cent. Pollen germinated to a very slight degree at both of these extremes, but the optimum concentration ranged between 35 and 45 per cent.

Temperature is an important factor in pollen germination, since at ordinary room temperature there was practically no germination, while if the cultures were placed in a warmer portion of the room, at a temperature of about 90° F. sometimes a high germination resulted. Other tests, carried on under as nearly identical conditions as possible, often gave entirely negative results. Tests made in an electric oven, at 95° F., showed at times a high percentage of germination, while at others the germination was very low. Although the proper conditions for germination could not always be produced, yet enough evidence was obtained to conclude that wherever any normal pollen is present, a portion of it is likely to have the power of germination, for in several cases where over 95 per cent of the pollen was abortive some of the morphologically perfect grains produced normal tubes.

BAGGING TESTS

The final test for the fertility of pollen is its behavior when used in pollination. The simplest method of testing pollen fertility is to bag the flowers before they open. This method has been used very extensively by several investigators in self-sterility studies of the pear, apple, cherry, peach, and grape and has been found to be efficient under favorable conditions. Observations by growers upon large blocks of any of the hermaphroditic varieties of strawberries agree that strawberries are all self-fertile, physiologically, wherever normal pollen is produced, so that the question of self-sterility does not enter into the problem.

Bagging tests were made on 106 varieties and 40 unnamed seedlings produced at the Minnesota Fruit Breeding Station. The detailed results and summary of these tests are given in Table X, and show (1) that in the hermaphroditic varieties studied no physiological self-sterility exists; (2) that wherever morphologically normal pollen is present fertilization takes place; and (3) that the extent of fertilization is dependent upon the percentage of normal pollen produced.

TABLE X.—*Degree of setting of the fruits of various positions on the inflorescence on 98 hermaphroditic varieties and 39 seedlings of strawberries when bagged*

Variety.	Number of stalks bagged.	Primary.			Secondary.			Tertiary.			Quaternary.			Number of flowers.	Total.		
		Perfect.	Nubbins.	Not set.	Perfect.	Nubbins.	Not set.	Perfect.	Nubbins.	Not set.	Perfect.	Nubbins.	Not set.		Perfect.	Nubbins.	Not set.
Abington	15	2	....	....	8	2	1	....	6	9	....	1	6	35	10	9	16
Abundance	5	....	3	....	2	5	3	2	5	15	....	3	10	48	4	16	28
Amanda	3	....	1	....	....	5	1	6	3	4	2	3	5	30	8	12	10
Arizona	2	....	1	1	....	4	....	2	3	1	....	....	3	15	2	8	5
Aroma	4	....	3	....	5	3	....	8	1	3	....	....	....	23	13	7	3
Barrymore	2	1	....	....	2	....	2	1	....	5	....	....	....	11	4	....	7
Bederwood	4	....	3	1	....	8	2	5	14	....	3	1	....	37	8	26	3
Bradley	5	....	1	2	3	9	5	7	3	8	....	1	11	50	10	14	26
Brandywine	3	....	2	....	10	....	....	8	4	5		4	....	36	22	6	8
Brown Beauty	3	....	2	1	....	3	5	6	4	7	....	2	7	3	6	11	20
Charles I	4	1	2	....	2	5	3	1	6	13	....	....	....	37	4	13	16
Chesapeake	4	2	2	....	6	5	....	8	4	....	....	4	2	33	16	15	2
Clara	1	....	1	....	2	1	....	3	....	1	....	....	2	33	5	2	3
Climax	4	2	1	1	12	....	....	14	1	2	....	2	2	10	28	4	5
Clyde	2	2	....	....	....	4	3	....	4	9	....	....	8	37	2	8	20
Cooper	1	1	....	....	1	3	....	....	....	....	....	....	....	30	2	3	....
Commonwealth	2	2	....	....	5	....	....	6	....	....	2	....	....	5	15	....	....
Corsican	4	3	2	....	1	4	7	3	4	15	....	....	3	15	7	10	25
Darlington	2	3	1	....	4	2	....	4	....	4	....	....	1	42	11	3	5
Dorman	3	....	5	....	3	5	2	3	2	1	....	1	4	19	6	13	7
Duncan	1	....	1	....	....	1	1	2	....	....	....	1	1	26	2	3	2
Early Jersey Giant	2	....	....	....	2	2	1	4	2	....	....	....	....	7	6	4	1
Early Ozark	2	2	....	....	3	1	1	1	....	3	....	....	....	11	6	1	4
Ekey	6	....	6	2	4	5	8	....	3	16	2	3	9	11	6	17	35
Enhance	2	1	1	....	1	2	2	....	3	3	....	1	2	58	2	7	7
Ewell Early	2	1	1	1	3	2	1	3	1	2	2	....	10	16	9	4	14
Excelsior	4	7	1	....	8	3	....	....	....	6	....	....	....	27	15	4	6
First Quality	6	2	2	1	9	5	....	12	6	2	5	....	3	25	28	13	6
Gandy	2	....	1	....	....	7	....	3	2	3	....	....	....	47	3	10	3
Gill	4	....	1	....	3	10	....	1	5	....	....	....	2	16	4	16	2
Glen Mary	1	1	....	....	4	....	1	1	....	1	....	....	....	22	6	....	2
Gold Dollar	5	4	2	1	9	4	2	12	1	....	1	1	5	8	26	8	8
Good Luck	2	....	2	....	....	7	....	4	4	1	....	2	4	42	4	15	5
Goree	1	....	1	....	1	1	1	1	....	11	....	....	....	24	2	2	12
Grand Marie	4	2	3	....	3	1	4	4	3	3	1	1	7	16	10	8	14
Hanbeck Beauty	3	....	4	1	....	7	3	....	3	7	....	....	....	32	....	14	11
Haverland [a]	2	....	....	....	4	....	....	2	....	....	....	....	2	25	8	6	....

[a] Not certainly true to name.

TABLE X.—*Degree of setting of the fruits of various positions on the inflorescence on 98 hermaphroditic varieties and 39 seedlings of strawberries when bagged*—Continued

Variety.	Number of stalks bagged.	Primary.			Secondary.			Tertiary.			Quaternary.			Number of flowers.	Total.		
		Perfect.	Nubbins.	Not set.	Perfect.	Nubbins.	Not set.	Perfect.	Nubbins.	Not set.	Perfect.	Nubbins.	Not set.		Perfect.	Nubbins.	Not set.
Ideal	7	4	3	2	7	7	11	2	4	18	....	....	6	64	13	14	37
Indiana	2	....	1	....	....	5	....	....	7	2	....	3	....	18	....	16	2
Jas. Todd	4	1	2	....	....	10	....	....	7	7	....	....	1	28	1	19	8
Jerome	4	....	1	1	3	3	5	....	3	15	....	....	19	50	3	7	40
Jessie	3	3	2	....	3	6	1	1	4	....	....	....	....	20	7	12	1
Jewell Imp	4	....	1	2	4	3	3	5	5	6	1	2	11	43	10	11	22
Joe	3	....	4	....	5	2	1	4	3	....	....	....	2	21	9	9	3
Kevitt Wonder	2	1	1	....	4	....	....	....	4	2	....	....	5	17	5	5	7
King Edward	4	1	4	1	5	4	7	4	2	10	....	....	....	38	10	10	18
Klondike	3	....	1	....	5	5	....	....	10	....	....	....	1	22	5	16	1
Late Jersey King	4	1	2	....	4	5	....	10	3	4	2	1	....	32	17	11	4
Lea	4	1	3	....	....	10	....	2	7	4	....	3	6	36	3	23	10
Longfellow	3	....	2	1	....	3	2	....	....	11	....	....	1	20	....	5	15
Lovett	4	....	2	2	....	8	1	1	11	2	2	2	2	33	3	23	7
Manhattan	8	....	6	1	2	19	2	6	28	3	....	....	3	70	8	53	9
Marshall	2	....	2	....	....	5	....	1	3	2	....	....	....	13	1	10	2
Mascott	4	....	5	....	....	14	....	2	7	7	....	....	1	36	2	26	8
Michell Early	1	....	....	....	....	1	1	....	7	....	....	4	1	14	....	12	2
Miller	3	....	2	....	....	10	1	4	11	5	....	4	8	45	4	27	14
Missionary	5	2	3	....	1	8	....	5	11	1	....	7	5	43	8	29	6
Model	2	2	1	....	....	3	....	5	6	....	3	....	....	20	10	10	....
Molinda	2	1	1	....	....	3	....	2	1	2	....	....	....	10	3	5	2
New Home	4	....	5	1	4	7	1	....	4	18	....	....	5	45	4	16	25
New York	4	....	5	....	....	1	9	1	3	8	....	....	....	27	1	9	17
Nich Ohmer	1	....	....	....	2	....	....	....	2	....	....	....	3	7	2	2	3
Ohio Boy	6	....	4	1	....	19	2	1	22	10	1	4	6	70	2	49	19
Orem	3	....	3	....	....	10	....	....	9	8	....	....	....	30	....	22	8
Oswego	6	3	1	....	....	13	3	....	6	21	....	1	1	49	3	21	25
Palmer	3	....	2	1	....	3	5	....	4	7	....	5	2	29	....	14	15
Pan American	6	1	3	1	1	5	7	....	12	9	....	6	20	65	2	26	37
Parson Beauty	4	....	6	....	....	6	11	....	8	13	....	....	3	47	....	20	27
Pearl	4	....	6	....	3	9	....	4	13	6	....	....	6	47	7	28	12
Pennell	2	1	....	....	5	....	....	....	4	2	....	....	7	19	6	4	9
Pineapple	4	....	5	....	2	9	2	....	6	5	....	....	1	30	2	20	8
Pitcher Eclipse	3	....	2	....	2	4	1	1	12	....	....	....	....	22	3	18	1
Pride of Delaware	4	1	4	....	5	8	....	5	6	10	....	1	6	46	11	19	16
Pride of Minnesota	6	2	6	....	2	12	1	....	14	7	....	9	9	62	4	41	17
Prolific	6	3	2	....	9	2	3	8	5	12	....	....	2	46	20	9	17
Providence	4	2	2	....	4	7	....	5	1	9	....	....	3	33	11	10	12
Reasoner 324	2	....	4	....	....	7	....	2	10	....	....	5	....	28	2	26	....
Rewatisco	3	1	2	....	5	4	....	4	6	1	....	....	....	23	10	12	1
Ridgway	3	....	3	....	4	7	....	4	6	5	....	....	....	29	8	16	5
Sample	3	2	1	....	1	4	2	....	11	3	....	....	12	36	3	16	17
Saratoga	2	....	2	....	1	5	....	....	5	8	....	....	3	24	1	12	11
Saunders	2	....	2	....	....	8	....	2	4	7	....	....	1	24	2	14	8
Senator Dunlap	2	2	....	....	2	1	1	2	....	4	....	....	4	16	6	1	9
Son's Prolific	4	....	3	1	5	6	....	6	4	6	1	....	11	43	12	13	18
South Dakota	3	2	2	....	3	4	....	3	2	8	....	1	7	32	8	9	15
Staples	4	3	2	1	5	4	2	6	1	11	1	....	5	41	15	7	19
Steven's Late Champion	5	....	4	....	3	10	1	4	9	15	....	1	6	53	7	24	22
St. Louis	3	1	2	....	....	8	....	....	2	4	....	....	....	17	1	12	4
Success	2	2	....	....	1	1	....	1	3	....	....	....	1	9	4	4	1
Tennessee Prolific	2	....	3	1	....	6	....	....	4	....	....	....	....	14	13	....	1
Three Ws	1	....	....	....	....	1	2	....	1	5	....	....	1	10	2	....	8
Twilley	1	....	2	....	....	5	1	....	1	2	....	....	....	11	....	8	3
Uncle Jim	2	1	2	1	....	4	4	....	1	5	....	....	5	23	1	7	15
Warfield	3	1	1	1	4	7	....	6	3	4	2	3	6	38	13	14	11
Warren	1	1	1	....	3	1	1	....	1	2	....	....	....	10	4	3	3
Wm. Belt	4	6	2	....	7	5	1	4	....	....	5	....	3	33	22	7	4
Winner	2	....	1	2	....	5	1	....	3	5	....	2	1	20	....	11	9
Wolverton	2	3	....	1	5	2	....	....	5	5	....	....	....	21	8	7	6
Minnesota 3	4	1	3	....	....	10	....	....	8	3	1	1	2	29	2	22	5
Seedling 14	2	....	1	2	....	2	4	....	....	8	....	....	7	24	....	3	21
Seedling 114	a 1	....	1	....	....	6	....	....	8	2	2	5	7	31	2	20	9
Seedling 130	a 3	....	4	....	1	4	5	3	2	6	1	2	4	32	5	12	15
Seedling 97	a 2	1	1	1	....	7	....	1	4	5	2	2	2	26	4	14	8
Seedling 15	1	....	....	....	....	1	3	....	1	4	....	....	2	11	....	2	9
Seedling 123	a 1	....	....	....	....	....	3	....	5	1	....	....	1	10	....	5	5
Seedling 123	b 1	....	....	....	....	....	....	....	....	....	....	....	....	11	....	....	....
Seedling 89	2	....	2	1	....	3	6	6	3	9	3	....	....	33	9	8	16

a One bag split or tip open, allowing the possibility of cross-pollination.
b Of a total of 11 flowers, none set. The pollen of this variety has not been examined.

TABLE X.—*Degree of setting of the fruits of various positions on the inflorescence on 86 hermaphroditic varieties and 39 seedlings of strawberries when bagged*—Continued

Variety.	Number of stalks bagged.	Primary.			Secondary.			Tertiary.			Quaternary.			Number of flowers.	Total.		
		Perfect.	Nubbins.	Not set.	Perfect.	Nubbins.	Not set.	Perfect.	Nubbins.	Not set.	Perfect.	Nubbins.	Not set.		Perfect.	Nubbins.	Not set.
Seedling 40	2	....	1	....	2	2	7	4	3	10	....	....	3	32	6	6	20
Seedling 168	2	1	....	3	....	2	6	....	....	4	....	1	5	22	1	3	18
Seedling 585	2	....	1	1	....	2	3	4	3	1	4	1	4	24	8	7	9
Seedling 753	[a] 2	....	3	....	....	4	1	4	3	2	1	....	4	22	5	10	7
Seedling 876	[a] 2	1	....	....	....	6	....	4	5	....	....	1	4	21	5	12	4
Seedling 703	1	....	1	....	....	3	....	1	1	4	....	....	4	14	1	5	8
Seedling 778	[a] 2	....	1	....	....	3	2	2	6	1	8	....	1	24	10	10	4
Seedling 937	2	....	4	....	....	5	2	1	8	3	....	5	2	30	1	22	7
Seedling 1065	2	1	2	....	3	3	....	3	5	2	2	....	3	24	9	10	5
Seedling 1009	2	....	1	....	....	7	....	2	1	3	1	1	2	18	3	10	5
Seedling 845	2	....	1	1	1	2	2	1	2	4	1	1	....	16	3	6	7
Seedling 901	1	....	1	....	....	2	....	....	1	1	....	....	....	5	....	4	1
Seedling 1018	2	....	2	....	....	2	3	....	3	6	....	....	....	16	....	7	9
Seedling 1017	2	....	2	....	2	2	....	6	1	....	....	....	....	13	8	5	....
Seedling 585	2	1	1	....	....	6	3	....	....	11	....	....	....	22	1	7	14
Seedling 702	2	....	2	....	....	3	1	1	2	7	....	1	4	21	1	8	12
Seedling 753	2	....	....	....	....	5	....	1	8	....	....	....	....	14	1	13	....
Seedling 778	4	3	1	....	5	2	....	7	2	....	....	2	1	23	15	7	1
Seedling 776	7	5	3	....	6	10	....	1	15	4	....	....	....	44	12	28	4
Seedling 908	2	1	3	....	4	2	3	4	....	2	3	....	....	22	12	5	5
Seedling 923	4	....	3	....	....	8	....	6	3	2	....	....	....	22	6	14	2
Seedling 924	1	1	....	....	....	3	3	....	....	6	....	....	....	13	1	3	9
Seedling 937	1	....	1	....	....	3	....	....	....	....	....	....	3	11	....	8	3
Seedling 947	3	....	3	....	1	6	2	....	8	....	....	....	1	21	1	17	3
Seedling 1010	5	....	5	2	1	7	11	....	7	15	1	....	8	57	2	19	36
Seedling 1017	3	....	4	....	....	4	5	4	7	....	....	....	....	24	4	15	5
Seedling 1023	3	3	....	1	8	1	....	10	....	2	....	....	....	25	21	1	3
Seedling 1026	2	....	....	1	....	4	....	1	2	2	....	....	6	16	1	6	9
Seedling 1045	1	....	1	....	....	2	....	....	2	2	....	....	2	9	....	5	4
Splendid×Dunlap	2	....	1	1	....	....	4	....	....	8	....	....	4	18	....	1	17
Total	....	113	160	48	285	624	234	337	587	646	70	114	410	....	....	....	....
Per cent	....	26.8	61.8	11.4	24.9	54.6	20.5	21.5	37.4	41.1	11.8	19.2	69	....	....	....	....

[a] Two bags split or tip open, allowing the possibility of cross-pollination.

Pollination in unbagged flowers is for the most part dependent upon bees and small insects and upon the anthers becoming erect and partially folding about the receptacle while dehiscing, thus dropping the pollen on the stigmatic surfaces. In the bagged flowers the insects are eliminated, and thus the most efficient natural means of pollination is lost. As a consequence many of the bagged varieties produced many nubbins, but no case of complete self-sterility was found where morphologically perfect pollen was present.

If the percentages of total perfect fruits, nubbins, and sterile flowers of each flower position in Table IV are compared with those in Table X, it will be seen that (1) the setting under bags is very much poorer than in the open, both with regard to the number of perfect fruits set and also with regard to the actual number of flowers which set any achenes, and (2) the primary flowers are decidedly more fertile than the later ones, as, even under the adverse conditions of pollination within the bags only 11.0 per cent of the primary flowers were sterile, while 20 per cent of the secondary, 40.7 per cent of the tertiary, and 68.5 per cent of the quaternary flowers were sterile, in spite of the very great increase in amount of

pollen present in the bags while the later flowers were in condition for pollination.

In order to determine to what extent parthenogenesis or parthenocarpy might possibly enter into the above results, bags were put over 67 clusters of 22 pistillate varieties. Of a total of 661 flowers covered, 55 set some achenes. Of these, 52 were found in 6 bags which had been accidentally split, thus accounting for the probable pollination by insects. Of the remaining three fruits, which developed in apparently tight bags, two bore 1 achene each and the other 7. Significance can hardly be attributed to the setting of these few achenes, since the chances for accidental pollination, to this extent, are relatively great. It may therefore be concluded that parthenogenesis does not exist in the cultivated strawberry.

A condition which might possibly be attributed to parthenocarpy occurred in the Buster variety, in which 9 flowers of the 22 bagged showed a very decided development of the achenes with no accompanying development of the receptacle. These achenes contained no embryos. In the strict sense of the word parthenocarpy in the strawberry could only be applied to a development of this kind. A more comprehensive use of the term might include the development of the fleshy receptacle. Ordinarily, flowers which set only one or a few achenes develop the fleshy receptacle only at corresponding points, due probably to the stimulus of fertilization. In perfect varieties receptacles are often found in which development has taken place not only at the base of the pistils but also about the base of the stamens. In 3 out of 10 bagged flowers of the pistillate Red Bird variety, the fleshy receptacle developed about the base of the staminodia forming a red fleshy circle about the dried pistils. Two flowers of Crescent, also an imperfect variety, developed normal fleshy berries, one bearing one achene and the other none. Apparently these receptacles developed without the stimulus of fertilization in the same way as that at the base of the staminodia in Red Bird.

POLLEN DEVELOPMENT

As Mendelian and, in fact, most genetic results are dependent upon the segregation of determiners during the formation of gametes and to their recombination again at the time of fertilization, any processes which interfere with the normal procedure should be carefully studied and, if possible, their nature determined.

There are a number of ways in which the normal order may be disturbed, at least there are various outward expressions of them. The condition in the *Phylloxera* spp., as pointed out by Morgan, in which half of the spermatids degenerate regularly, while the other half continue and form normal spermatozoa, and the relationship between degeneration and the absence of the accessory chromosome is so well known that it needs no comment. Gates (*18*) has shown that in

Oenothera lata the early abortion of the male generative organs and partial abortion of the female is in some way associated with the presence of an extra chromosome, while in *Oenothera semilata* an extra chromosome is present, but only a portion of the pollen grains abort. Morgan has shown that slight mutations are continually occurring in *Drosophila* spp., which inhibit the development of the 2X individual, while Bridges (*5*) has shown that certain chromosome combinations can not bring about normal development in the zygote. Is it too much to expect that like conditions may affect the 1X generation also?

Dorsey (*12*) pointed out a different type of pollen degeneration from that which expresses itself in the production of empty grains. He showed that in functionally pistillate grapevines pollen developnemt proceeds normally through the microspore division and the formation of the normal content of cytoplasm found in mature fertile grains. During the period of development following the microspore division, one or both of the nuclei of a portion of the pollen grains aborted, leaving the grain normal as far as cytoplasm was concerned. Associated with the complete sterility of the pollen of the functionally pistillate varieties were the reflexed type of stamens, an entire lack of sutures and germ pores in the mature pollen, and dieciousness. It is probable that the lack of germ pores is the direct cause of sterility in the numerous grains which otherwise appear entirely normal. Tischler, Rosenberg, and others have shown that pollen abortion in hybrids may follow either normal or irregular reduction divisions, when the parents have both an equal and unequal number of chromosomes. Shull (*35*, *36*) has recorded some consistent irregularities in sex ratios in *Lychnis dioica* which will later be shown possibly to have been due to slight mutations causing pollen abortion. Goodspeed (*21*, *22*) gives further evidence on the sterility of hybrids of *Nicotiana* spp,,when *N. sylvestris* is used as one parent and shows that not only the pollen is sterile but that the F_1 plants are incapable of forming any very appreciable amounts of seed. Rimpau (*31*) and Jesenko (*26*) have shown that in hybrids between wheat and rye there is complete male sterility, while some of the egg cells are able to produce viable seed if pollinated with either wheat or rye pollen.

The cytological investigation of pollen development in the strawberry, reported in this paper, has two main objects in view: (1) the determination of the mechanism and nature of pollen abortion and with these facts at hand, (2) the determination to which of the many categories of sterility the very prevalent pollen abortion in the strawberry varieties belongs.

MATERIAL AND METHODS.—The variety used as the basis of this study is Minnesota 3. As was previously stated, it furnishes desirable material for this type of study, as about 50 per cent of its pollen aborts, while the remainder develops normally. The egg cells in this variety and in the cultivated varieties in general do not show a corresponding

degree of abortion, as it is very common for practically all of the achenes to develop on perfectly formed strawberries.

The material was prepared for microscopic examination according to the ordinary cytological methods. Carnoy's, Flemming's strong, medium, and weak, and chromacetic-acid fixing solutions were used. All gave very good results, except Carnoy's fluid. Sections were cut from 4 to 20 μ thick, the best results being obtained from those 4 to 6 μ thick. The triple stain and Haidenhain's iron-alum-hymatoxylin stains were used, both giving good satisfaction.

The drawings in Plates B to E were outlined with the help of an Abbe camera lucida. All, with a few exceptions noted, are drawn to the same scale, in order that comparisons of cell size and cytoplasm content may be readily made.

ANTHER TISSUES.—The walls of the young anthers are made up of four oblong layers of cells of about equal size; the outer epidermal layer and three inner layers. Inside of these layers there is usually one layer of tapetal cells and about five layers of pollen mother cells, both of which at this time are easily distinguished from the wall cells by their large size and different staining reaction.

The growth and development of the wall layers should be followed because of its relation to the increase in size of the pollen mother-cell cavity during the formation of the tetrads. As the pollen mother cells prepare for reduction, and during the division, rapid cell division is taking place in the parietal cells, so that by the time the heterotypic division is complete there is an appreciable increase in the size of the anther cavity. Gradually the two inner layers of cells flatten out, owing probably to the growth of the outer layer, the cells of which rapidly increase in size, although showing no further cell divisions.

At the tetrad stage the inner layer is very much flattened, while the middle layer is still plainly visible and the cells are still full of cytoplasm. The cells of the outer layer are now very appreciably larger than the epidermal cells, which have also grown slightly. After the liberation of the microspores and while they are increasing in size, the epidermal cells sometimes collapse, as their contents have become scant. By the time the microspores have nearly completed their growth and have begun to divide, the cells of the outer layer have become deeper than long and are nearly as large as the tapetal cells. At this time they show distinctly the spiral thickenings which have to do with dehiscence. Both of the inner layers have now collapsed or show very scant cytoplasm. Before dehiscence the walls separating the members of the two pairs of loculi break down, leaving two large loculi in each anther. The relation between the increase in size of the anther cavities both during preparation for the first meiotic division and subsequent to it, and a difference which *Fragaria* spp. shows from some other forms in the history of the mother-cell wall will be pointed out later.

THE TAPETUM.—The tapetum, usually one cell layer thick, is composed of large angular cells similar in size, and staining reactions to the pollen mother cells. The tapetum in *Fragaria* spp. differs in its greater persistence from most other forms reported. Division in the tapetal cells begins at about the time of synapsis of the pollen mother cells and has been observed as late as the metaphase of reduction division. The divisions are all mitotic, no evidences of amitotic divisions having been observed. Following reduction division the tapetal cells are binucleate and remain so until the liberation of the microspores, when they degenerate and completely disappear. The disappearance of the tapetal layers is gradual. They first separate from the wall layers and then proceed to dissolve, the wall which was in contact with the anther wall first disappearing, followed by gradual dissolution of the entire cell layer. During this process the walls become thick and laminate and in places the middle lamella dissolves, partially freeing the individual cells. When the microspores are three-quarters grown the tapetal cells have entirely disappeared. This persistence of the tapetal cells will be shown to be correlated with a like persistence of the pollen mother-cell walls. The history of the tapetum in *F. virginiana* is identical with that just described which is of Minnesota 3.

POLLEN MOTHER CELLS.—The study of pollen development was begun with the so-called resting stage of the pollen mother cells between the last archesporial division and the first meiotic division. They do not, however, show the characteristic chromatin and linin condition found in true resting cells of *Fragaria* spp. (compare fig. 1, Pl. B and fig. 2, Pl. D). The cells are angular and contain a large nucleus (Pl. B, 1). The contents of the nucleus are irregular dark-staining, very small masses of chromatin held in a network of linin fibers. The number of chromatin bodies is very much larger than the number of chromosomes. Ordinarily one large nucleolus is present, although it is not uncommon to find two.

SYNAPSIS.—The first indication of the onset of the prophase is to be seen in the gradually increasing size of these chromatin bodies which still, however, appear very flaky and irregular. The linin and chromatin during this period are so indistinct that it is impossible to determine whether there is any definite pairing of the individual particles and threads as has been shown to exist in *Lilium* spp. by Allen (*2*) and in several forms by Overton (*30*). These larger masses gradually move to one side of the nuclear cavity and congregate about or near the nucleolus in a loose indefinite mass (Pl. B, 2). At this time a few rather definite threads appear in the mass, some extending out from it as loops. Where the loops are long enough, they are seen to be distinctly double (Pl. B, 2, 3). This is the only evidence of any pairing during the presynaptic stages. Gradations between the conditions shown in figures 1 and 2 occur within a single loculus of an anther and are proof

that these stages bearing bivalent loops are presynaptic. Gradually the synaptic mass tightens until it is close and compact, occupying a very small portion of the nuclear cavity (Pl. B, 4). During this contraction there are refractive particles present both in the mass, some of which are in contact with the nucleolus, and outside of the nuclear membrane, which give the same staining reactions as the nucleolus. Similar masses to these Digby (*11*) has considered to be synaptic extrusions.

The synaptic stage is of long duration. Gradually the chromatin in synapsis takes on the appearance of being made up of a closely tangled mass of threads. Soon loops are pushed out from it, which are bivalent often for their entire length (Pl. B, 5). The fact that these loops are often double from the point at which they leave the mass to the point of entrance, and can sometimes be traced through a portion of the synaptic mass gives the impression that they are made up of two continuous threads which closely approximate each other over their entire length. This view is supported by the later stages, especially those at and following segmentation, which in *Fragaria* spp. are very clear.

Loops continue to push out from all sides of the synaptic mass, often shifting it to the center of the nucleus. Gradually the bivalent thread becomes more or less regularly distributed about the nuclear cavity, usually having, however, a somewhat tangled center near the nucleolus. The spireme thread at this stage often appears to be a single strand due to the close approximation of its univalent portions (Pl. B, 6). However, no anthers at this stage of development have been found which do not contain many portions of the spireme which are double for considerable distances. It is probable that, during the post synaptic stages up to segmentation of the spireme into chromosomes, the univalent portions of the thread are never fused throughout their whole length to form a single spireme. It is even possible that no fusion takes place, but that the univalent threads only approach each other so closely that in such delicate threads the line of demarcation can not be distinguished.

There is no distinct second contraction, but there is a semblance of one following the loosely-distributed spireme stage. The thread contracts gradually but unevenly throughout its whole length, its univalent portions as a consequence becoming separated from one another and appearing thicker (Pl. B, 7). The portions of loops which are in contact with the nuclear membrane remain so and often extend long distances on the periphery and then turn at relatively sharp angles and again extend in fairly straight lines toward the central mass, still situated usually near the nucleolus. Many of the loops in this way form equilateral triangles. There is no doubt at this time of the double nature of these loops. The paired threads are evidently identical with those which appeared while passing out of synapsis and may be identical with the bivalent loops seen extending out from the loose presynaptic

mass. Continued contraction of the bivalent spireme results in segmentation.

SEGMENTATION.—In order to determine definitely whether a telosynaptic or a parasynaptic arrangement of the univalent chromosomes prevails during the synaptic and postsynaptic stages, it would seem necessary to determine the exact procedure from the bivalent condition just previous to segmentation, through segmentation to the paired condition in diakenesis. If it can be shown that the bivalent threads appearing during the pre and post segmentation stages are identical in *Fragaria* spp., it will be a strong argument in favor of the parasynaptic arrangement of the chromosomes. As *Fragaria* spp. is not complicated by a second contraction and, as the segmentation stages are rapid, all stages from that shown in Plate B, figure 7, to diakenesis being found within a single loculus; and as the stages during this period are unusually distinct, such a determination is not difficult.

Digby (*11*) has recently presented the results of a very detailed study of the cytology of *Crepis virens* in which the conclusion is reached that there is an end-to-end arrangement of the chromosomes during the synaptic stages. The details from the loosening of the synaptic mass to segmentation are very similar to those in *Fragaria* spp., although the chromatin in *C. virens* is apparently much more viscous and gives less clear-cut images than does *Fragaria* spp. Her figures 76, 78, and 79 may be considered as in the same stages as my figure 7 of Plate B and to present the same condition—that is to say, a split or a double spireme the pairs of which are somewhat twisted about one another. She considers that these figures do not show two univalent threads lying side by side, but that the bivalent loops are due to the folding back upon each other of univalent segments during second contraction. At this stage the chromatin mass became so viscous that—

> it is generally impossible to individualize the future three bivalent chromosomes. The chromosomes are in fact evolved out of what appears to be a tangle of viscous nuclear contents.

It appears hardly logical to conclude from this evidence that there is an end to end rather than a side to side pairing of the univalent chromosomes.

The number of loops present at segmentation in species of Fragaria is always less than the number of chromosome pairs which appear at diakenesis. It has been mentioned that these loops extend for long distances on the periphery of the nucleus, forming more or less regular equilateral triangles. When segmentation takes place, it is usually at the outer angles of these loops and at or near the nucleolus, which generally forms more or less of a center from which the loops radiate. Thus the bivalent loops are often divided into three pairs of bivalent chromosomes (Pl. B, 9). The pairs continue to contract, those attached to

the periphery remaining in that position and those which have one end attached to the nucleolus assuming a position alongside of it (Pl. B, 11, 14). Occasionally one pair may be attached both to the nucleolus and to the periphery; when there is evidence of considerable force exerted by the pair in contraction (Pl. B, 11). The pairs continue to contract (Pl. B, 12, 13), forming various figures which have often been described in other forms, but very few circles have ever been seen at this time. The contraction continues until the typical diakenesis stage is reached when it is often difficult to distinguish between the two univalent chromosomes of a pair (Pl. B, 14, 15). Apparently they often fuse, as in the multipolar spindle stage they sometimes appear as single entities. At diakenesis 26 chromosome pairs can readily be counted. At this stage in Minnesota No. 3, of 22 counts made, 19 showed definitely 26 chromosome pairs and three others showed, respectively, 24, 25, and 27.

A very similar condition to the diakenesis of the pollen mother cells is shown in the prophase of the tapetal cell divisions. Here, however, in place of the 26 pairs of chromosomes 52 pairs appear arranged about the periphery of the nucleus. Five counts made at this time showed in three cases 52, and in two 50 and 54 pairs, respectively.

HETEROTYPIC DIVISION.—Diakenesis in the pollen mother cells is of somewhat long duration, but the period between it and the metaphase of the heterotypic division is extremely short, usually not more than two or three multipolar spindles appearing in a loculus simultaneously. The small oval chromosomes now arrange themselves on the equatorial plate. Whether there is any definite order or arrangement could not be determined, as the chromosomes appear identical. They are arranged close together and, while their number can not be readily determined, 26 have been counted on one plate and 24 on another.

The chromosomes are then gradually pulled apart and drawn to the poles. No irregularities in cell division or extrusion of chromatin matter have been seen during this process. The daughter chromosomes show only slight evidence of fission for the following division. The disk-shaped daughter nuclei are soon formed (Pl. C, 1), and directly after prepare for the second meiotic division.

HOMEOTYPIC DIVISION.—The two spindles of the homeotypic division may be parallel to one another or their axes may be at right angles. The metaphase of the division is also characterized by great uniformity, the daughter chromosomes separating and advancing toward the poles simultaneously. After separation they could be readily counted and showed in 7 counts 26 chromosomes (Pl. C, 2).

The daughter nuclei are soon formed, and walls are laid down between them, dividing the cytoplasm evenly. The cells gradually split apart, separating the four microspores and allowing the entrance between them of the viscous material which has up to this time surrounded either

partially or entirely the original mother cytoplasm (Pl. B, 9; Pl. C, 1, 3, 4).

POLLEN MOTHER CELL WALL.—The history of the pollen mother cell wall is of interest as it differs somewhat from that generally reported for the higher plants.

In the lily (*Allen, 1*), grape (*Dorsey, 12*), and in many other plants in which pollen development has been studied, it is usual, during preparation for the first meiotic division, for the pollen mother cells to separate from one another, due apparently to dissolution of the middle lamella and to growth of the anther walls, forming a greater space into which the cells can round up and float free from one another. Allen (*1, p. 200*) considers that the separation is due to a dissolution of the cell walls from between the mother cells, and that each is "surrounded only by a plasma membrane." Following separation, a very decided thickening of the material surrounding the cytoplasm takes place (Pl. B, 9; Pl. C, 1). This, Allen (*1*), Tischler (*41*), Stevens (*38*), and others speak of as a thickening of the mother cell wall. Following the formation of the tetrads, this material increases and, as the cells of the tetrad separate from one another, flows between them. This material is usually of a rather firm nature and in buckwheat (*38*) often persists for some time after the liberation of the microspores from it.

There is evidence in *Fragaria* spp. which indicates that this material is entirely distinct from the mother cell wall and is in no way dependent on it for its increase in volume, thus appearing to be more of the nature of the gelatinous sheath which surrounds groups of cells in many of the algae.

In *Fragaria* spp., in place of the pollen mother cells rounding up just before or during reduction division, while there is taking place a rapid growth of the anther walls and a consequent increase in size of the anther cavities, the cytoplasm separates at the angles from the walls and rounds up independently (Pl. B, 9, 14, 15; Pl. C, 1). The walls remain in contact with one another and adjust themselves to the increasing space by stretching. As soon as evidence of rounding up of the cytoplasm appears, a gelatin-like material is secreted unevenly about the cytoplasmic mass (Pl. B, 9; Pl. C, 1). This material is apparently identical with that laid down about the plasmic mass in the grape, lily, and forms like them in which the mother cell wall rounds up, supposedly following the dissolution of the mother cell wall. In these cases it is generally spoken of as the thickening of a new mother cell wall. In the strawberry this material increases in amount until at the completion of tetrad formation and before liberation of the microspores, the spores are completely embedded in it (Pl. C, 3, 4). The mother cell walls are still present, but simply divide the anther cavity into large spaces, which are only partially filled by the tetrad (Pl. C, 3). An examination of analogous stages to these in the lily and

grape shows the mother cell wall lying closely about the gelatinous material in which the spores are embedded, it having not disappeared at the period of rounding up of the pollen mother cells, as is generally assumed. At the time of rounding up of the pollen mother cells in these two plants, there is no evidence of old walls being left behind, but there seems rather to be a separation of the contiguous walls, due to the dissolution of the middle lamella and rounding up of them with the plasma masses. The walls give a slightly different staining reaction from the thick secreted mass and so can be readily distinguished from it. During the liberation of the spores in the grape, it is not uncommon to see this gelatinous sheath completely disappear, leaving portions of the original mother cell wall about the spores. This gradually dissolves, liberating the spores. In the strawberry, the procedure is much the same. The gelatinous sheath, which shows no wall closely about it but only a limiting membrane, dissolves, liberating the spores into the large cell bounded by the mother cell wall. This soon disappears.

At the time of liberation the spores have a distinct wall about themselves, which is independent of the surrounding sheath. Apparently the condition in the lily, grape, and strawberry is identical, as far as structures are concerned, but differs primarily in the separation of the walls of contiguous cells in the former plants, while in the latter only the cytoplasm of the pollen mother cells rounds up, leaving the walls and middle lamella intact.

Following the liberation of the tetrads and the disappearance of the mother cell walls, degeneration of the tapetum takes place. Tapetal degeneration seems to be in some way correlated with the disappearance of the middle lamella from between the mother cell walls, for in those forms which show an early rounding up of the mother cell walls there is a correspondingly early degeneration of the tapetal cells.

GROWTH OF THE MICROSPORES.—Following the liberation of the microspores, there is a period of very rapid growth in their walls. At first this causes the microspores to become very irregular in outline (Pl. C, 7), but as growth continues and the wall becomes thicker the cells become more spherical. The growth of the microspore wall is so rapid that there is not a corresponding growth of the cytoplasm, a condition which results in a large vacuole occupying the greater portion of the cell cavity. When growth of the microspores is nearly complete, the original cytoplasmic content of the spore is spread out over the periphery of the cell and about the nucleus (Pl. C, 8). The comparative size and consequently the very great decrease in relative cytoplasmic content, of the newly liberated microspores and those ready for the microspore division may be realized by comparing figures 5 and 8 of Plate C, which are drawn to the same scale.

Early in the development of the liberated microspore the wall is differentiated into the extine and intine (Pl. C, 7). The extine gradually

thickens and a series of scales are formed over its surface. The external appearance of the extine is shown in Plate C, figures 15 and 16; Plate D, figures 6 and 15. Soon after the microspore division the extine development is practically complete.

DIVISION OF THE MICROSPORE NUCLEUS.—With the growth of the microspore there is an apparent decrease in chromatin content; for, in the nuclei which are just about to divide, the chromatin is distributed in small particles about the periphery of the nucleus and appears very scant. Transition stages between that seen in Plate D, figure 8, and the completion of the spireme have not been observed. The spireme (Pl. D, 9, 10) is a continuous, heavy, dark-staining thread. It follows, more or less, the periphery of the nucleus and surrounds the large nucleolus which has at this time begun to break down. The nucleolus takes on a very irregular outline, which is in some way related to the numerous threadlike processes which extend from it to the spireme thread (Pl. D, 10). The nucleolus is now very light-staining and seems for the most part homogeneous, but it may contain one or more small vacuoles. Soon after the segementation of the spireme into its 26 constituent parts the nucleolus completely disappears.

Following segmentation of the spireme the nuclear membrane disappears, the chromosomes are drawn to one plane, and the spindle is formed (Pl. D, 11). The most usual position of the spindle in the microspores of many plants is near the wall and perpendicular to it; the pole which is to form the generative nucleus being nearly in contact with it. As a result of this position the generative cell usually lies against the wall and the vegetative nucleus in the cell cavity (Pl. D, 15). This arrangement of the spindle is also found commonly in *Fragaria* spp., but is not universal. Often spindles are found which lie parallel to the wall (Pl. D, 12) and result in the arrangement of the nuclei shown in Plate D, figure 14, both of which lie against the wall.

The spindle is always broad at the poles and short. The chromosomes on the equatorial plate are small and oval in shape and may readily be counted if a section can be obtained in which the heavy wall of the microspore is removed both above and below the chromosomes. In these sections 26 chromosomes are plainly visible. The daughter chromosomes are drawn to the poles simultaneously (Pl. D, 12), no instances having been seen in which chromosomes lagged behind on the spindle or in which there was an extrusion of chromosomes.

Directly after the rounding up of the daughter nuclei and the disappearance of the spindle fibers there is visible no sign of a cell wall or limiting membrane (Pl. D, 13) between the two nuclei, which is eventually to set off the generative nucleus in a separate cell (Pl. D, 14, 15). Soon, however, the wall appears and the generative cell begins to round up (Pl. D, 14), eventually to lie free in the cytoplasm of the pollen grain (Pl. C, 1).

POLLEN MATURITY.—After the microspore division there is again a period of growth of the pollen grain and a very marked increase in the amount of cytoplasm. Eventually the pollen grain is completely filled with cytoplasm of a distinctly alveolar structure. During this time the cytoplasm nearly disappears from about the microspore nucleus, leaving the microspore cell wall loosely surrounding the nucleus, the chromatin of which is gradually taking on the condition typical of resting nuclei (Pl. D, 2).

When pollen formation is complete, changes take place in the anthers preparatory to dehiscence. These consist primarily in breaking down the wall between each pair of loculi, thus throwing all of the grains of one-half of the anther together. There is also a general drying-out process which results in the disappearance of the liquid material which previously surrounded the developing grains, and of a considerable portion of moisture from the pollen grains, thus causing them to collapse along three meridial sutures which fold in, thus giving in cross section somewhat of a clover-leaf shape, while the general shape of the grain is long-oval. The three germ pores are located at the middle points of the sutures. On placing the dry pollen in water it soon swells to form a sphere.

The position of the generative cell and vegetative nucleus within the collapsed grains could not be determined, for as soon as the killing fluid penetrated the anthers the grains immediately swelled. In the swelled grains the nuclei lie in various positions with regard to one another, but usually in close proximity. The vegetative nucleus is generally spherical while the generative cell contents are fusiform, owing to the folding of the dried pollen grains and are not closely surrounded by the cell wall. The chromatin of both nuclei now shows the typical resting condition (Pl. D, 2).

Up to and including the liberation of the microspores from the tetrad, the cells have shown marked regularity in division, the stages of short duration proceeding regularly from one end of a loculus to the other, while during the stages of longer duration the cells of a loculus all show the same degree of development. Up to the time of liberation of the microspores, the development which has taken place has depended entirely on materials furnished by the sporophyte, the one group of chromosomes merely being the tools by which the materials of the pollen mother cell were divided into four parts, the microspores. So far as can be seen up to this point, no growth process resulting directly in an increase of cell material can be directly attributed to the one aggregation of chromosomes. At the time of liberation from the tetrad the spores are strikingly alike in size and all other visible characters. There has been, up to this time, no differentiation in rate of development of individual microspores; and the spores, as liberated, are all normal.

DEGENERATION OF THE MICROSPORE

Liberation of the microspore from the tetrad places these individuals upon their own resources for future development. It is true that the spores are surrounded by a nourishing medium furnished by the sporophyte, but the ability to use this material depends upon the individual cell metabolism of the microspores.

A study of the actual change in cytoplasmic content from the pollen mother cell stage to the stage of complete formation of the pollen grains indicates the degree to which the young spores are dependent upon their own metabolism from the time of liberation from the tetrad to maturity of the male gametophyte or mature pollen grain. Measurements were made of the diameter of the spherical cytoplasmic mass at the following stages during pollen formation: Rounded pollen mother cell at diakenesis, young microspores which have just been liberated from the tetrad, microspores which have completed growth and in which the nuclei are either dividing or are about to divide, and the mature pollen grains. A summary of the measurements is given in Table XI. It will be seen by comparing the volume of the pollen mother cells and of the microspores at liberation that the latter show slightly less than one-fourth the volume of the former, indicating that during reduction division and the period subsequent to the liberation of the microspores no increase in cytoplasm has occurred. Following liberation from the tetrad, however, when the microspores are floating in the nourishing medium of the loculus as independent units, very rapid wall growth takes place. From the time of liberation to division of the microspores nucleus the volume of the cells increases about 6.4 times, but shows no corresponding increase in cytoplasm. At the mature pollen stage the cells have increased to nearly 7.5 times that of the liberated microspore. The changes in volume and cytoplasmic content from the pollen mother-cell stage to mature pollen are also well illustrated by Plate B, figure 14; Plate C, figures 4 and 8; and Plate D, figure 2, all of which are drawn to one scale.

TABLE XI.—*Volume of pollen mother cells and microspores at various stages of development*

Stage.	Number measured.	Average diameter.	Volume.
		μ.	*Cu. μ.*
Pollen mother cell at diakenesis	263	15.25	1,859.99
Liberated microspores	300	9.41	436.28
Microspores, division stage	200	17.44	2,777.40
Mature pollen	500	18.39	3,255.39

Although the gametophytic generation must properly be considered as beginning with the first appearance of the haploid chromosome number, yet the liberation of the spores from the tetrad may be considered as marking the beginning of the independent growth period of this generation and the rapid growth of the spore wall, division of the microspore nucleus, the increase in cytoplasm, and finally the germination of the pollen grain and the production of sperms as developmental stages in this very much foreshortened plant generation. The very rapid wall growth, division of the nucleus, and finally the increase in cytoplasm to 7.5 times its original volume, all within a relatively short period, go to make this period of a plant's life history probably the most finely adjusted and critical one which it is called upon to survive.

It is during the periods of rapid enlargement and of increasing cytoplasm that degeneration of the microspores takes place.

Although there is some evidence in the strawberry that degeneration may begin before liberation of the microspores from the tetrad, so many anthers have been examined which contain only normal microspores, both in the tetrad stage and directly following their liberation, that degeneration before this time can be considered as negligible. It is probable that poor fixation may account for the few apparent instances which have been found. Indeed, poor fixation constantly enters as a disturbing factor in the interpretation of the condition of the supposedly aborting grains, and it is only by finding the same types at later and more advanced stages of degeneration when there can be no question as to the condition of the microspore that the factor of poor fixation can be eliminated. No aborted microspores have so far been found which could be referred to as degeneration within the tetrad.

Directly following microspore liberation evidences of pollen abortion may be noticed and from this period on through the various stages of development, microspores and pollen grains are continually aborting.

Plate D, figures 3 and 4, shows microspores shortly after liberation, in which the contents have completely broken down into a yellow oily mass which turns black on exposure to osmic acid. The lighter areas are globules evidently of a different substance.

Ordinarily during the growth period of the wall following liberation, the cytoplasm becomes spread over the periphery in a thin layer. Plate D, figures 5, 6, and 7, represent various conditions in which this normal process has not occurred. Figures 7 and 11 are later stages of this type of abortion in which degeneration of the nucleus and cytoplasm is gradually taking place. Figure 15 apparently represents a further stage of this series, in which the nucleus, although visible in outline, is, with the cytoplasm, entirely functionless. Plate E, figure 11, shows the completely degenerate microspore of this type found among normal mature pollen. The dark-staining mass is yellow and oily before killing.

Although there has been a considerable amount of degeneration up to the time of the completion of growth of the microspore wall, probably more takes place between the time of the formation of the large vacuole (Pl. C, 8) and the completion of the microspore division than at any other period.

Plate D, figure 12, shows a full-grown microspore in which degeneration is taking place, both in the cytoplasm and in the nucleus. This was found in an anther containing full-grown 1-nucleate microspores, and probably is a case in which degeneration has begun during the period of enlargement.

Plate D, figure 13, and Plate E, figure 2, represent early stages in degeneration of 1-nucleate microspores which are at the stage at which division should take place as they were found in anthers containing both 1- and 2-nucleate grains, as well as division stages. The microspore represented in Plate E, figure 7, was found among microspores of the stage of development shown in Plate C, figure 15, while that of Plate E, figure 8, was found among mature pollen grains. Both are evidently later stages of the condition represented in Plate D, figures 12 and 13, and Plate E, figure 2.

During the period of division a few microspores contain a very scant amount of cytoplasm. Such spores are seen in Plate D, figures 14 and 16, and Plate E, figures 1 and 4. Eventually these completely degenerate. Those of the type shown in Plate D, figure 16, and Plate E, figure 1, probably are the forerunners of the completely degenerate microspore shown in Plate E, figure 10, which is a common type in mature anthers.

Although degeneration takes place to a greater or less degree at all stages, from microspore liberation to microspore nucleus division, no instances of degeneration occurring during the process of division have been noted. Directly following division, however, evidences of degeneration again become apparent, although much less numerous than in the period just prior to division. Figure 3 of Plate E represents an early stage of degeneration directly following microspore division. This is probably an early stage of the more advanced degeneration stage shown in Plate E, figure I. This young pollen grain was found among grains in which the cytoplasm was increasing rapidly in amount. It will be noticed that the generative cell is aborting, while the remainder of the grain is normal. Apparently grains of this type continue to increase normally with regard to the vegetative portion, while degeneration of the generative cell occurs. Figure 13 of Plate E represents such a grain found in a mature anther. Figure 12 represents another type of degeneration which takes place subsequent to division of the microspore nucleus. The generative cell has completely degenerated. The vegetative nucleus, although still present in outline, is functionless, while the cytoplasm bears no resemblance to the normal. It still retains the property, however, of

absorbing liquids when placed in them, and so the grains of the type shown in Plate E, figure 13, are likely to cause inaccuracies when the ordinary methods of determining the percentage of good and abortive pollen are employed.

It seems clear thus far that degeneration of the microspores and pollen grains is a phenomenon closely related to the very active metabolic processes which are taking place during this period of the plant's life history.

DISCUSSION OF RESULTS

Thus far there has been shown to exist in the strawberry types of sterility due to at least two distinct causes.

In some of the wild species, including *F. elatior*, *F. platypetala*, *F. cuneifolia*, and *F. chiloensis*, it seems highly probable that the species are diecious, while *F. virginiana* is unquestionably so for the most part. Dieciousness is expressed in the production of pistillate plants bearing staminodia, which, so far as I have observed, never produce pollen. The staminate plants bear normal stamens and pistils, which appear normal but which seldom are fertile. Certain types are also found which are intermediate between these two types. A few staminate plants may bear fruit on one or more of the early flowers. These flowers may or may not bear stamens, but both staminodia and intermediate anthers are found on them. Other plants which are apparently staminate develop only intermediate anthers in which abortion takes place at the tetrad division or shortly after, resulting in a degenerate mass in the anther. Another staminate type has recently been studied which bears fruit on the primary and occasionally on some of the other flowers. The anthers of the primary flowers are reduced to staminodia. The secondary flowers carry pollen development through to the liberation of the microspores when 40 to 80 per cent of them abort and degenerate completely, forming a yellow oily mass. The remaining grains develop normally and are fertile. These types are all found in plants of pure *F. virginiana* and represent varying degrees of expression of dieciousness.

The diecious condition of the wild species from which the cultivated forms have been derived probably explains the greater sterility of the later flowers of the cultivated hermaphroditic varieties, than is found in those of the pistillates; if we can accept the origin of the hermaphrodites as being from males which have developed partial fertility of the female organs. The appearance of staminodia showing varying degrees of development in the cultivated varieties is also the direct result of dieciousness, while the intermediate types of anthers in the cultivated forms are of the same nature as those found in wild staminate clones. It is an interesting fact, in connection with the problem of sex determination and dieciousness, that where intermediate anthers or staminoids occur, either on wild clones or cultivated varieties which are able

to bear normal anthers, they are practically always borne on the primary flowers, while the anthers produced later have a greater tendency toward normal development. The tendency toward the production of staminodia is much greater in the early spring than later. On the other hand, pistil sterility is much more frequent on the later flowers of an inflorescence and when fruits set on wild staminate clones it is practically always on the first flowers of a cluster which open.

A second type of sterility often associated with the above type but due to a different cause is that which results in aborted microspores and pollen grains in otherwise normal anthers. Aborted pollen has been shown to be present in relatively small amounts in pure species of Fragaria, but appears often in large quantities in many of the cultivated varieties. This type of abortion has long been recognized in hybrids, and recently Jeffrey and his students have gone so far as to consider any plant bearing over 15 or 20 per cent of this type of pollen a hybrid.

Selfed seedlings and F_1 plants of crosses between varieties of cultivated strawberries are so extremely variable for many factors that it seems self-evident that they are of hybrid origin, and this is to a great extent confirmed by what is known of the origin of the numerous cultivated varieties, many of which are the result of variety crosses, while by far the larger number are chance seedlings. It thus seems evident that pollen abortion in the cultivated varieties is due to the same causes which produce sterility in other hybrids.

As would be expected, there are varying degrees of sterility resulting from hybridization and varying degrees of irregularities in the stages which lead up to the final abortion of pollen. There appear in the literature numerous instances of abortion in both male and female reproductive organs following irregular reduction divisions. The irregular divisions, especially in the pollen mother cells, result in the production of more than four cells of unequal size in the tetrad. These produce microspores of varying sizes, few of which ever come to maturity. Gates (*17, p. 98*) pointed out that most of the forms studied by Wille (*44*) showing supernumerary cells in the tetrad are either hybrids or have been under cultivation for some time and are open to the suspicion of being hybrids. Other plants, some of which are known to be hybrids while others which have been cultivated as horticultural varieties and are under suspicion as hybrids, have been studied in more detail by various workers. Tischler (*40, 41, 42*), who has done much work with plants of this type, finds that in hybrids of *Ribes* spp. and in the sterile hybrid *Mirabilis jalapa* × *M. tubiflora* pollen degeneration usually takes place following normal divisions. In the hybrids *Potentilla tabernaemontani* × *P. rubens*, *Syringa chinensis*, and *Bryonia alba* × *B. dioica*, and in three varieties of banana (*Musa paradisiaca*) having different chromosome numbers, irregular divisions are common and are always followed by much pollen abortion. In these banana varieties, the

origins of which are unknown but which differ cytologically in having 8, 16, and 24 chromosomes as the reduced number, it is significant that the most frequent irregularities in cell division during reduction, and most complete pollen sterility occurs in the two varieties having the greater chromosome numbers. Thus, pollen abortion may or may not be the result of irregularities at reduction division, but is apparently related to hybridity and is associated with heterozygosity.

After working with several hybrid plants showing both normal divisions and irregularities during reduction and formation of tetrads, Tischler (*41*, *p. 144*) concluded that—

> Die Sterilität bei Hybriden hängt nicht von irgendwelcher Chromatin repulsion ab.

He concluded further that irregularities during tetrad division can not be considered as characteristic only of hybrids. He thought that sterility of hybrids was due to the coming together of two sex cells which did not contain identical developmental tendencies and that these were expressed at the critical time of the formation of the reproductive organs. Actual abortion of the grains he thought was due to insufficiency of cytoplasm in the enlarged microspores.

One of the most striking cases of sterility following hybridization, the cytological details of which have been worked out, is that of the hybrid *Drosera longifolia* × *D. rotundifolia*, reported by Rosenberg (*33*). The striking feature of this hybrid is that it is between parents having different chromosome numbers, the diploid number of *D. longifolia* being 40, while that of *D. rotundifolia* is only 20. As a consequence the hybrid contains 30. At reduction division in both the megaspore mother cells and pollen mother cells there appeared 10 pairs of chromosomes and 10 single ones, the pairs supposedly being made of the 10 *D. rotundifolia* chromosomes paired with 10 from the *D. longifolia* parent, while the 10 single chromosomes were the remaining 10 *D. longifolia* chromosomes. Reduction division resulted in the separation of the paired ones, these being drawn regularly to opposite poles. The unpaired chromosomes, on the other hand, were either drawn to one or the other pole or were left in the cytoplasm to form another small nucleus. The homœotypic divisions took place normally. Following the organization of the microspores within the tetrad, many proceeded to increase in size; in some, division of the microspore nucleus proceeded normally, and then in practically all cases abortion of the pollen took place. Following tetrad formation in the female reproductive organs, three of the tetrads usually aborted, as is common, while the other proceeded to form the egg sac. Egg-sac formation was carried to various stages, but it was only very rarely that a perfect egg sac, capable of further development, was formed. Rosenberg concluded (*p. 39*) that because of the fact that the microspore division was able to proceed normally, the degeneration of the pollen grains was not the result of the irregular distribution of chromo-

somes during reduction division, but was due to a lack of cytoplasm. The abortion of the egg sacs, he again concluded, was not due to irregular divisions, as all of the divisions following reduction were normal, but was due to poor nutrition.

Nakao (*29*), working on the cytology of certain grain hybrids in which very striking irregularities in reduction division took place, followed by complete abortion of the microspore after liberation, concluded that abortion in this case was due to an insufficiency of cytoplasm previous to reduction division which resulted in abnormally early division and consequent irregularities. He did not consider why these irregularities should cause abortion of the microspores.

In view of the conditions existing within an anther at the time of degeneration of microspores and because of certain genetic results which can only be explained on the basis of selective elimination of certain gametic combinations, it is difficult to agree with the conclusions of Tischler and Rosenberg that degeneration has nothing to do either with the irregularities or normal repulsion which occur at reduction division in hybrids.

Although there are striking differences in the regularity with which reduction takes place in sterile or partially sterile hybrids, there are certain conditions, in both those which proceed normally and those which show irregularities, which are alike and must be taken into account in the consideration of the causes of pollen abortion. These conditions are as follows:

(1) At reduction division there is a sorting out of the parent chromosomes, resulting in new combinations in the daughter cells, the mnuber of which depends upon the degree of difference between the two parents. If division proceeds normally, there is an equal number of chromosomes in each daughter nucleus. If it takes place irregularly, unequal numbers are found in the resulting daughter cells. In either case the combinations are new and may or may not contain all of the properties necessary for perfect metabolism of the cell.

(2) If divisions take place regularly, there is an equal quantitative and, as far as can be determined, also an equal qualitative division of cytoplasm between the quadrants of a tetrad. If divisions have proceeded irregularly, the cytoplasm is divided between the members of the tetrad in proportion to the amount of chromatin which they contain. In either case at the time of liberation from the tetrad, or if liberation does not take place, as in *Drosera* spp., at the period previous to enlargement, all of the microspores appear normal—that is, they contain an organized nucleus and are filled with cytoplasm. In Minnesota 3 there is at this time as great uniformity in size and cytoplasmic content of the individual microspores as is found in entirely fertile plants of *F. virginiana*.

(3) It is not until rapid growth of the microspores takes place and the necessity of active cell metabolism appears that evidences of degeneration appear. The necessity of active metabolism becomes apparent when it is remembered that the microspores increase 7.5 times their original volume during this growth period.

(4) There is no specific time at which degeneration of the grains within a single anther takes place. In most of the sterile forms thus far studied a series of degenerating stages appear from the first period of growth of the microspores to the formation of nearly mature pollen.

It is becoming more and more evident that the growth and development of plants and animals are directly dependent upon the chromosome combination which they contain. Boveri (*see Morgan, 28, p. 55*), in working with dispermic sea-urchin eggs, found that they very rarely develop normal individuals, while if separated at the 4-celled stage normal individuals often developed. This seems dependent upon the fact that in the first four cells, which are the result of a single division, the chances of one of the cells receiving at least one of each kind of chromosome are relatively high and thus, when separated, some may develop normally. On the other hand, the chances of each of the four cells receiving one of each kind of chromosome necessary for perfect development are small; and as a result the individual develops abnormally. Bridges (5) has shown that in the fruit fly *Drosophila ampelophila* certain variations from the normal chromosome combinations have a definite effect upon the development of the zygote. Zygotes containing 3X chromosomes die, while those containing 2X and a Y chromosome develop normally. Male individuals may develop which contain an X but no Y chromosome, but were found to be entirely sterile; while those zygotes which received only a Y chromosome died as did also those which received 2Y chromosomes, but no X. Zygotes containing 2Y chromosomes plus an X, however, were able to develop into normal males. Apparently the presence of an X chromosome is necessary for the development of an individual, while the presence of a Y in males is necessary if the male is to be fertile.

In plants the evidence for the dependence of development upon chromosome combinations is becoming indisputable if the Mendelian interpretation of the inheritance of factors is admitted. In F_1 progeny of hybrids, if the parents are homozygous, there is generally as much uniformity as is shown by either parent, while the F_2 progeny shows a wide range of types, often overstepping the limits of the parents. If such a variety of types with regard to hardiness, rust resistance, adaptability to various regional and soil conditions, and vigor of the individual plant are produced in the 2X generation as the result of new chromosome combinations, why is it not possible for a similar series to exist in the 1X generation with regard to the ability of the individuals to develop in a given environment?

I have already pointed out that up to the time of liberation of the microspores from the tetrad, in the strawberry, cell divisions have resulted merely in an equal division of the cytoplasm of the original mother cell between its four granddaughter cells with no evidence of any metabolic changes resulting in an increase of cytoplasm. A similar condition exists in those forms which show irregular divisions during reduction with uneven distribution of cytoplasm between the resulting cells. Liberation of the microspores from the tetrad marks the end of the period of dependence of these cells upon the 2X generation, as far as future growth and development is concerned. At this time there is no difference between the conditions surrounding the microspores of a hybrid and those of a genetically pure individual. Both groups of microspores are set free in a homogeneous anther sap to complete their own further development.

The progress of the developmental stages in plants of pure *F. virginiana* is characterized by great regularity of development of the individual microspores within a loculus with regard to rate of enlargement, time of division of the microspore nucleus, and the subsequent development of cytoplasm. In fact, there is as great uniformity shown in these stages as was shown in the stages leading up to the mature tetrad stage in either *F. virginiana* or Minnesota 3. Minnesota 3, on the other hand, shows great irregularities during this developmental period in rate of growth of the individual microspores, in the time of division of the microspore nucleus, and in the rapidity of formation of cytoplasm. This lack of uniformity is in striking contrast to the uniformity shown in earlier stages of the same plant, while the cells were dependent on the 2X individual. The liberated microspores of Minnesota 3 are strikingly uniform in size and cell contents.

During any period, following liberation of the microspore to the completion of development, microspores or pollen grains may be found degenerating. As all of the grains within a loculus are free in a homogeneous nutrient liquid, it seems difficult to believe that the variations in development can be due to anything but the individual constitution of the microspores.

Indeed, there is constantly accumulating an increasing amount of evidence which points to the continual elimination of gametes bearing certain chromosome combinations. In 1894 Millardet (27) reported on a series of hybrids between species of strawberry the progeny of which, he said, formed an exception to the general rule of hybrids, as the specific type of one or the other parent was always produced in the first and later generations. The specific type shown in the second generation was, with one exception, the same as that shown by its parent in the F_1 generation. Millardet mentions complete sterility in one species of cross and high percentages of sterility in the F_1 generation of some of the other combinations. Bellair (3) reports that in the tobacco cross *Nicotiana*

sylvestris × *N. tabacum* the F_1 generation resembled the *N. tabacum* parent and was partially fertile. From these he was able to obtain F_3 plants apparently identical with the two parents and fully fertile. The reappearance of types similar to the parents in large numbers in the F_3 generation suggests the elimination of gametes containing combinations which would result in intermediate types.

Detlefsen (*10*), working with animals, reports results obtained from cavy crosses which may readily be explained on the basis of the elimination of certain combinations in the gametes of the males. He crossed tame females to wild males. The F_1 males were all sterile. The cross F_1 female with wild male was not very successful and produced one sterile male and a sterile female. The F_1 females crossed to tame males gave sterile males of which a few produced some nonfunctional sperms. The females of this back-cross again crossed to tame males produced males showing a low degree of fertility. As this process was continued, always crossing back to tame males, the fertility of the male progeny increased as they became more nearly homozygous for the tame condition. In the sixth generation all of the males produced sperms, and 66.7 per cent of these males were readily fertile. Apparently the more chromosomes of one parent type which were present in the sperm, the greater its chance of complete development.

East (*13*) in a short abstract gives the conditions which he found in the progency of the partially sterile hybrid *Nicotiana rustica humilis* × *N. paniculata*. The F_1 progeny of this hybrid were very uniform, but only 1 to 6 per cent of the female gametes were functional, and 2 to 6 per cent of the pollen grains were morphologically perfect. In the F_2 generation some perfectly fertile plants were found, many possible F_2 combinations were omitted, many more homozygous combinations occurring than should be expected, and the parent types appeared once in every 100 to 200 plants, whereas if all of the possible F_2 combinations appeared, the parent types would be much more rare. East considered that the results might be explained on the basis either of selective elimination of F_2 zygotes or selective elimination of F_1 nonfunctional gametes. He considered further that the elimination of the nonfunctional gametes might be due to irregularities of chromosome distribution, which scheme seemed improbable; or the facts might be interpreted without this assumption if certain conditions were met which are as follows:

If (1) there is a group of chromosomes in each parent that can not be replaced by chromosomes from the other parent; if (2) there is a group of chromosomes from each parent, a percentage of which may be replaced by chromosomes from the other parent, but where functional perfection of the gametes varies as their constitution approaches that of the parental forms; if (3) there are other chromosomes that have no effect on fertility and therefore can promote recombinations of characters in the progeny of fertile F_2 plants; if (4) a naked male nucleus entering the normal cytoplasm of the egg in the immediate cross can cause changes in the cytoplasm that will affect future reduction divisions; if (5) this abnormally formed cytoplasm is not equitably dis-

tributed in the dichotomies of gametogenesis in the F_1 generation; if (6) it follows from (4) and (5) that F_2 zygotes may be formed which are less perfect in their gamete forming mechanism than those of the F_1 generation; and if (7) the heterotypic division of gametogenesis does not necessarily form two cells alike in their viability.

In the strawberry, in which no irregular distribution of chromatin occurs, certain of these assumptions—namely 1, 2, 3, and 7—would apply in explaining partial male sterility in many partially sterile varieties, but assumptions 4 and 5 and assumption 6, which is dependent upon them, can hardly be considered applicable; assumption 4 because there is no cytological evidence that there has been any disturbance of reduction division; 5, because there is apparently equal distribution of the mother cell cytoplasm to each member of the tetrad, and 6, because there is no cytological evidence which would lead one to believe that the cytoplasm of the zygote had anything to do with the perfection of its gamete forming mechanism. In the strawberry sterility seems to be due to the inability of certain chromosome combinations to use the food material in which they are embedded in the growth and development of the liberated spore to a ripe pollen grain.

If we can accept the hypothesis of pollen abortion being due in hybrids to certain chromosome combinations affecting the normal metabolism of the microspore in its development, the question at once presents itself: Is pollen abortion the result of the presence of one particular chromosome or of certain combinations of two or more, or do all of the chromosomes play some part in it? This question can not be answered from the facts so far obtained in the strawberry because of the heterozygous condition of the material which has been used; but there is other published evidence which throws some light on this question.

Belling (4) has made a very careful study of partial sterility of hybrids between four species of the "bean" Stizolobium. He found that the F_1 plants, of those crosses in which the velvet bean (*S. deeringianum*) was used as one parent continually, aborted one-half of the pollen grains and one-half of the egg sacs. Of the second generation plants one-half were completely fertile and one-half partially sterile, as in F_1. The progeny of fertile F_2 plants continued to be fertile, while the progeny of the partially sterile plants were one-half fertile and one-half partially sterile. Belling explained these results on the basis of the presence in the velvet bean of the factor K, which was not present in the other three varieties. These three, however, contained the factor L not present in the velvet bean. The presence of either K or L he assumed to be necessary for the normal development of either egg sacs or pollen grains, the presence of both K and L causing abortion. We may extend this working hypothesis slightly and put it on a chromosome basis, in which case we must consider that Belling's factors K and k form one allelomorphic pair, being situated in a certain loculus of a specific chromosome in the velvet and the other three varieties of beans, respectively, and that the factors

L and l form an allelomorphic pair located in a definite but different chromosome of the three varieties and the velvet bean, respectively. Then, to follow out Belling's scheme, the presence of the chromosomes bearing the factors K and L in the same member of a tetrad causes abortion, and likewise the presence of both chromosomes lacking the factors K and L causes abortion. Belling states that abortion of the microspores takes place in the vacuolate stage and that there are no intermediates between the completely aborted and the most perfect grains, thus strengthening the idea that in this case no more than two chromosomes have to do with abortion.

Another set of studies which point to one instead of two chromosomes being the cause of pollen abortion are those of Shull (*35*, *36*) on the inheritance of sex and of a sex-linked factor in *Lychinis dioica*. In the first of these studies Shull showed that very probably *L. dioica* ♀ is homozygous for the sex determining factors, while *L. dioica* ♂ is heterozygous. In crossing these forms an approximate ratio of 1 pistillate to 1 staminate usually resulted, but with nearly always a slight excess of pistillate plants, suggesting, if the females are homozygous for sex, an elimination of a portion of the male gametes bearing the determiner for maleness. In a later study he was able to show that the determiner for maleness was linked with a factor for narrow leaves while in normal plants the determiners for femaleness were linked with broad leaves. In a narrow-leaved mutant male found by Baur he showed that the determiner for femaleness as well as maleness was linked with the narrow-leaved determiner. It was as a result of the discovery of this homozygous (for leaf width only), narrow-leaf male that the factor for narrow leaves linked to maleness was able to be discovered as, being a recessive character and always in a heterozygous condition, it was hidden in normal males.

When these homozygous narrow-leaved males were used in crosses with either normal broad-leaved females or heterozygous females, there was always produced a great excess of males, the females appearing only in very small numbers. These results were apparently in contradiction to those previously obtained in which females were more abundant. Shull gave no explanation of these irregularities. They suggest, however, that there is a fairly constant elimination of certain gametes. A study of all of Shull's results, with this idea in mind, indicates that an explanation based on the elimination of certain male gametes will cover all cases of irregularity so far reported by him except the nonappearance of homozygous hermaphrodites and of heterozygous hermaphrodites containing male determiners. These two instances, if we may draw analogies between plants and animals, are of the same nature as the YY zygotes in species of Drosophila, and die (*Bridges*, *5*).[1]

[1] Shull (*35-36*) has shown that the hermaphrodites have undoubtedly been derived from males; and therefore the presence of two hermaphrodites or a male and an hermaphrodite determiner would be analogous to the presence of two male determiners.

In every other instance in which irregularities in sex ratios occurred, a male or hermaphroditic parent was used in which the condition for narrow leaves was linked with either a determiner for maleness, femaleness, or hermaphroditeness. If the irregularities were relatively slight, as was the case when normal broad-leaved males and females were crossed, maleness and narrow leaf were linked. A partial elimination of these male gametes would produce the actual results obtained. Hermaphrodites of *Lychnis dioica* acted in the same manner as the males. Hermaphrodites of *Melandrium album*, which we may assume to bear the narrow-leaf and hermaphrodite determiners linked, as they have undoubtedly been derived from males, acted in the same manner as the narrow-leaved males—that is, they produced only females when crossed to normal broad-leaved females, in place of a 1 to 1 ratio. These results can be explained on the assumtion of complete elimination of the male gametes of the *M. album* hermaphrodite, which carry the hermaphrodite mutant and its linked factor, narrow leaf, and in the case of the narrow-leaved *L. dioica* males of the nearly complete elimination of the male gametes bearing the mutant factor for femaleness and narrow leaf.

In all cases it seems that the factor for narrow leaves has an inhibiting action on the formation of the male gametes and results in the partial or complete elimination of them. Elimination in the normal males is not complete; otherwise this line would long ago have disappeared. In the mutants in which narrow leaf is linked with femaleness, elimination of male gametes bearing this mutant factor is nearly complete. Shull has also given much evidence which shows that there is also some elimination of female gametes bearing this mutant factor but to a less extent than in the males. Such partial elimination of the female gametes was shown in the cross heterozygous broad-leaved female (of the formula FBFb) by a narrow-leaved male Fbfb, which produced two heterozygous broad-leaved females, no homozygous narrow-leaved females (the nearly complete absence of both of these classes evidently being due to the elimination of male gametes bearing the factor for narrow leaves and femaleness), 630 broad-leaved males, and 463 narrow-leaved males. In this cross all four types should have appeared in equal numbers.[1] The

[1] The effect of the linked factors "narrow leaves" and "femaleness" on the production of male and female gametes can be most readily seen by the use of this simple diagram

♀ \ ♂	Fb	fb
FB	Fb FB 2	fb FB 630
Fb	Fb Fb 0	fb Fb 463

in which the male gametes are placed on the upper side of the square and the female gametes on the left side, while the number of each of the types of progeny are placed within the small squares, with their respective gametic combinations.

inequality of the last two classes must be due to inequality in production of the two kinds of female gametes FB and Fb; the latter, which carries femaleness and narrow leaf linked, appearing less frequently than FB. Apparently with the suppression or loss of the determiner for broad leaves in the sex chromosome, there has also been a partial suppression of a factor necessary for the normal development of male and to a less extent of female gametes. In personal correspondence with Dr. Shull he informs me that there is actually a great deal of pollen sterility in the narrow-leaved Lychnis male.

CONCLUSIONS

(1) The flowers of Fragaria are pentamerous with regard to all parts except pistils. The stamens are arranged in three whorls; the outer parapetalous series of 10 stamens, the middle antipetalous, short filamented series of 5, and the inner antisepalous series of 5. Increases in stamen number are due to the addition of 5, or a multiple of it, to either the antipetalous or the antisepalous series. Decreases in stamen number are due to the loss of first the antipetalous and next the antisepalous series. Apparently the parapetalous series are permanent. Decrease in stamen number is in no way related to dieciousness.

(2) There is a positive correlation between flower position, flower part number, and size of fruit in the strawberry.

(3) The wild American species of strawberry, from which the cultivated varieties have been derived, are for the most part diecious. The pistillate plants bear staminodia, which rarely develop as far as the pollen mother cell stage, and the staminate plants bear pistils which superficially appear to be perfect but which are only occasionally functional. In a few wild clones of *F. virginiana*, which appear to be sterile, pollen development is carried as far as the tetrad division or slightly beyond this to the liberation of the microspores, when complete disintegration of the anther contents to an oily mass takes place. In other instances a portion of the microspores develop normally while the remainder within the same anther disintegrate, while in other clones shortly after liberation, and following a slight growth of the microspores, complete abortion of the same type as that found in hybrids takes place. These anther types, in wild clones, all appear to be various expressions of a tendency toward dieciousness and are not the result of hybridization. Similar anther types are common in certain cultivated varieties, on the early flowers of an inflorescence, and especially on those appearing early in the season.

(4) There is a correlation between flower position and fertility of pistils, fertility decreasing in the later flowers of an inflorescence. Pistil sterility is expressed in the production of irregularly shaped berries or entirely sterile flowers. Sterility of the later flowers of an inflorescence is more general in hermaphrodites than in pistillates, suggesting that the hermaphrodites have been derived from staminates of the diecious wild forms.

(5) The appearance of considerable amounts of aborted pollen in wild plants of *F. virginiana* and *F. americana* is rare except in anthers of the intermediate type. Most cultivated varieties produce considerable amounts of aborted pollen of the type common in hybrids. The percentage of aborted grains is not constant in the individual flowers of a variety, and neither is it constant in the individual anthers of a single flower, as just as great variations appear within the anthers of a flower as are shown by composite pollen samples of individual flowers.

(6) In those varieties producing high percentages of aborted grains a portion, at least, of the morphologically normal pollen grains are functional, as shown by germination and bagging tests. There is no evidence of a physiological self-sterility in the strawberry.

(7) In the partially sterile variety Minnesota 3 pollen development is carried on normally up to the liberation of the microspores from the tetrad. At this time all of the microspores appear normal and alike. Following liberation, variations in rate of growth, time of division of the microspore nucleus, and ability of the individual microspores to develop normally are shown. At all stages, during this growth period microspores were found in various stages of abortion. *F. virginiana* exhibits as great regularity during this growth period as is shown in the stages leading up to liberation of the microspores.

(8) Liberation of the microspores from the tetrad marks the beginning of an independent gametophytic generation, so far as the metabolic processes of growth are concerned. The individual microspores float in a homogeneous nourishing medium provided by the sporophyte, but the use of this food material in cell metabolism depends entirely upon the individual organization of the microspores.

(9) Specific chromosome combinations have been shown by various investigators to be a potent factor in the development or lack of development of individual plants or animals. In plants heterozygous for a number of factors, as are the varieties of strawberries, numerous new chromosome combinations occur for the first time in the microspores. The varying rates of growth, time of microspore division, ability to increase the cytoplasm, and inability in many cases to develop normally seem to be the outward expression of the differential ability of these new chromosome combinations to carry on cell metabolism.

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PLATE B

Minnesota 3:

1.—Pollen mother cell previous to synapsis. × 2,000.

2.—Presynapsis in the pollen mother cell showing loops extending out from synaptic mass. × 2,000.

3.—Two loops and portion of a loop extending from the presynaptic mass. Same stage as figure 2. × 3,280.

4.—Synapsis in a pollen mother cell. × 2,000.

5.—A postsynaptic stage. The synaptic mass is unraveling into bivalent loops. × 2,000.

6.—Open spireme stage. × 2,000.

7.—A presegmentation stage of the spireme. × 2,000.

8.—A portion of a bivalent spireme thread of the same stage as figure 7. × 3,280.

9.—Segmentation of the bivalent spireme into chromosome pairs. The cytoplasm is rounding up and is partially surrounded by a gelatin-like sheath. × 2,000.

10.—A portion of the bivalent spireme during segmentation. × 2,340.

11, 12.—Chromosome pairs during the contraction period following segmentation. × 2,000.

13.—Individual chromosome pairs showing various figures commonly formed during contraction. × 3,280.

14.—Diakenesis in the pollen mother cell. × 2,000.

15.—Multipolar spindle stage of pollen mother cell. × 2,000.

16.—Early anaphase of the heterotypic division. × 3,280.

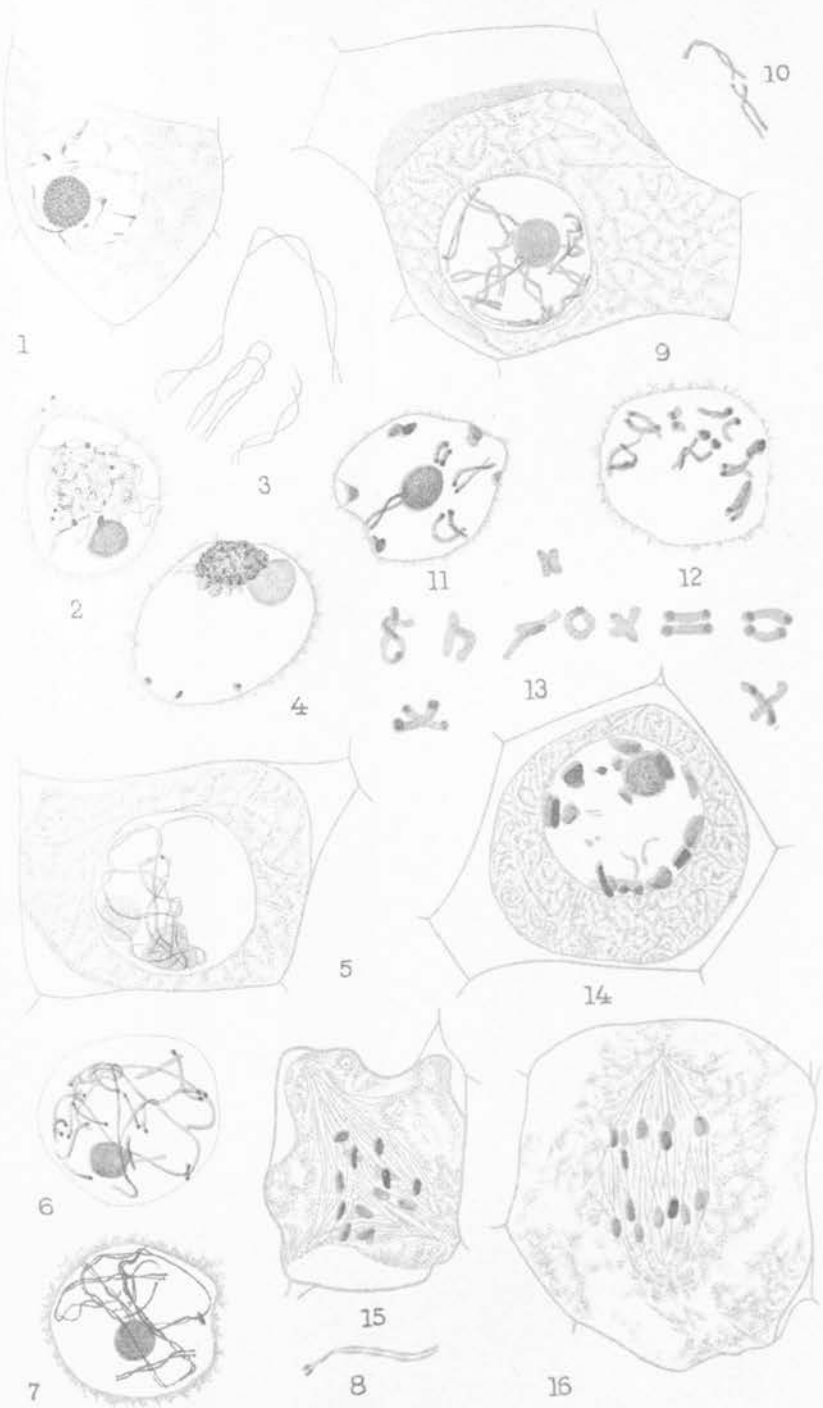

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PLATE C

1.—Late anaphase of the heterotypic division. The cytoplasm is rounding up from the mother cell wall and is partially surrounded by a thick gelatin-like sheath. × 2,000.

2.—Chromosomes on the equatorial plate of the homeotypic division.

3.—A portion of an anther in the tetrad stage, showing the microspores embedded in the gelatin-like sheath. The original mother cell walls are still present.

4.—A tetrad at the same stage as those shown in figure 3. The mother cell wall is not shown. × 2,000.

5.—A microspore shortly after liberation from the tetrad. × 2,000.

6.—A liberated microspore in which growth has commenced. × 2,000.

7.—A later stage than figure 6, showing the slight thickening of the wall and the irregularities due to growth of the wall. × 2,000.

8.—Microspore growth completed previous to division of the microspore nucleus. × 2,000.

9.—A section through a microspore nucleus in prophase showing the continuous univalent spireme. × 3,280.

10.—Another section of the same nucleus, showing the first stages of the disappearance of the nucleolus. The nucleolar strands are attached to the spireme. × 3,280.

11.—Metaphase of the division of the microspore nucleus. A spindle in this position results in the nuclear arrangement shown in figure 15. The thickened extine is shown. × 2,000.

12.—*F. virginiana.* Anaphase in the division of the microspore nucleus. The spindle lying parallel to the wall results in the nuclear arrangement shown in figure 14. × 2,000.

13.—Telophase of the division of the microspore nucleus. The wall which eventually surrounds the generative nucleus is not always apparent at this time.

14.—A later stage than figure 13 in which the generative cell has been definitely cut off. × 2,000.

15.—A young pollen grain shortly after division, showing an increase in cytoplasm content. The thickened extine is shown. × 2,000.

16.—End view of a pollen grain showing the pattern of the laminate layers shown in figure 15 and Plate D, figures 1, 6, and 15. The arrows mark the ends of the three sutures which bear the germ pores.

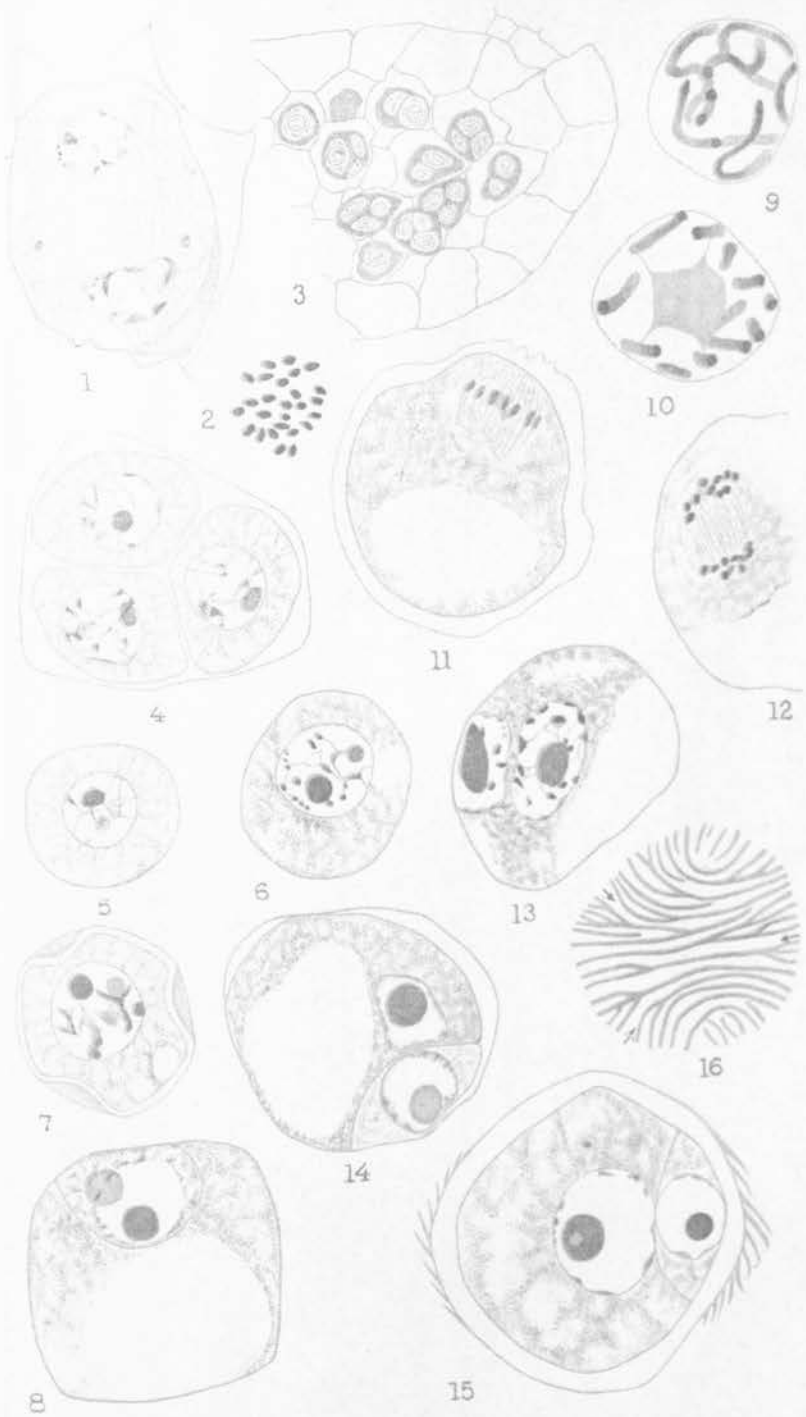

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PLATE D

1.—Nearly mature pollen grain. The central body is the vegetative nucleus while the other is the generative cell. × 2,000.

2.—Mature pollen grain. The extine is not shown. The killing fluid causes the dry folded grains to become spherical. × 2,000.

3, 4, 5, 7.—Various types of degenerate microspores from anthers bearing microspores of the stage shown in Plate C, figure 6. × 2,000.

6.—An aborting microspore from an anther containing half-grown microspores. × 2,000.

8.—An aborting microspore of the same type as that shown in figure 6 from an anther containing nearly full-grown microspores as in Plate C, figure 8. As in Plate D, figure 6, the cytoplasm and nucleus still appear normal. × 2,000.

9, 11.—Microspores of the same types and same age as figures 6 and 8, in which degeneration has proceeded farther. × 2,000.

10.—An aborted microspore from an anther containing microspores of the stage shown in Plate C, figure 8. Apparently abortion took place shortly following liberation from the tetrad.

12.—An early stage of degeneration in a full-grown 1-nucleate microspore. × 2,000.

13.—An early stage of degeneration in a full-grown 1-nucleate microspore. A number of normal microspores in this anther are already dividing.

14.—An aborting microspore containing an abnormally small amount of light staining cytoplasm; from an anther containing 1- and 2-nucleate microspores. × 2,000.

15.—An aborted microspore from an anther containing 1- and 2-nucleate microspores. Apparently this is a late stage of the type of degeneration shown in figures 6 and 8. × 2,000.

16.—An aborted microspore containing very scant cytoplasm. The nucleus has completely degenerated and degeneration of the cytoplasm has begun.

PLATE D

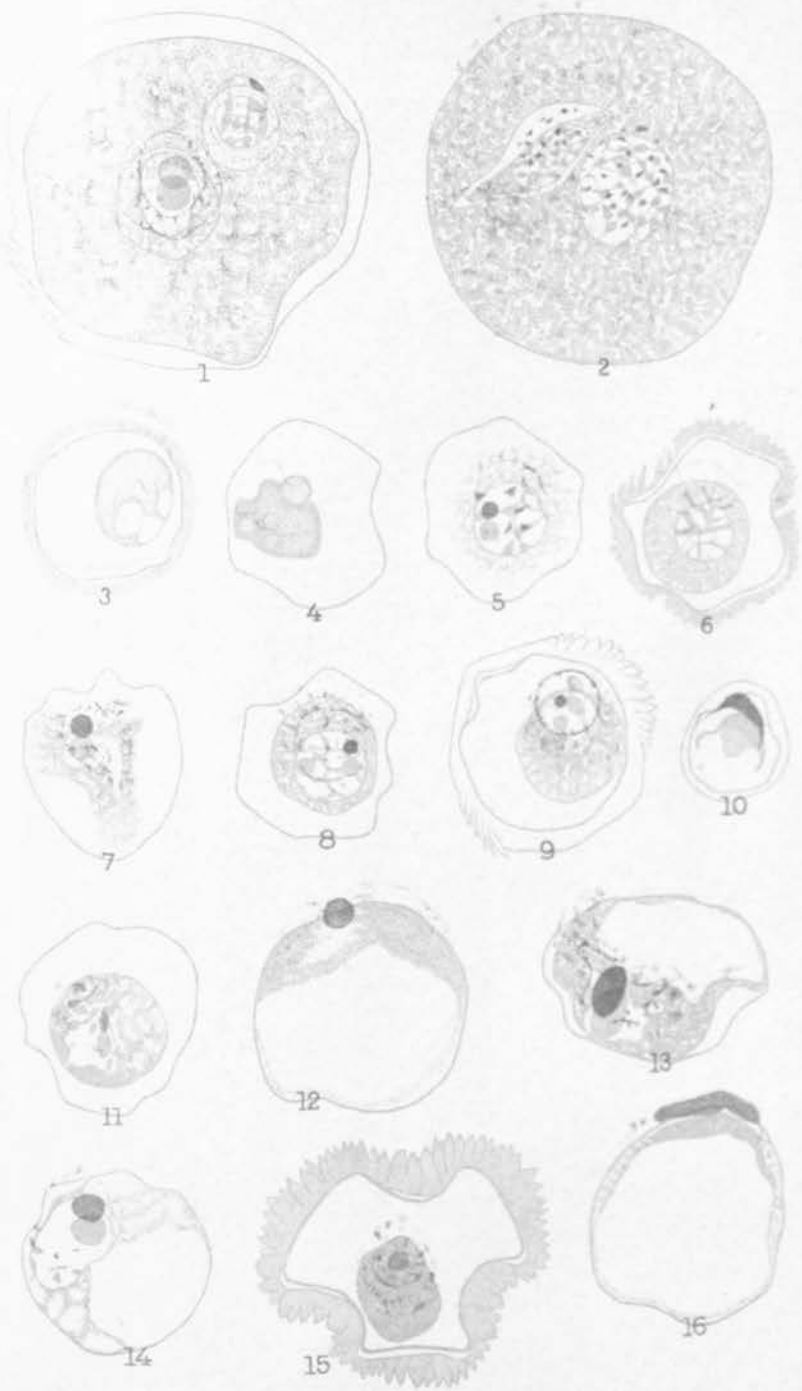

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PLATE E

1.—A slightly more advanced stage of the condition shown in Plate D, figure 16.

2.—An early stage in the abortion of a full-grown 1-nucleate microspore. × 2,000.

3.—An early stage of abortion directly following microspore division. × 2,000.

4.—A full-grown 1-nucleate microspore containing very scant light-staining cytoplasm; from an anther containing 1- and 2-nucleate microspores. × 2,000.

5.—Another type of degeneration of a full-grown 1-nucleate microspore. × 2,000.

6.—An aborted microspore found among 1- and 2-nucleate microspores. × 2,000.

7.—A later stage of the type of degeneration shown in Plate D, figure 13; from an anther containing microspores of the stage of development shown by Plate C, figure 15. × 2,000.

8.—Degeneration of the generative cell shortly after division. The vegetative nucleus and cytoplasm are still normal. × 2,000.

9, 10.—Common types of aborted microspores found with mature pollen. Evidently abortion took place before the division of the microspore nucleus. × 2,000.

11.—An aborted microspore, of the same type as that shown in figure 7. Found with mature pollen. × 2,000.

12.—A pollen grain showing abortion of the generative cell and an abnormal vacuolate condition of the cytoplasm. × 2,000.

13.—A later stage of the type of degeneration shown in figure 8. The vegetative nucleus and cytoplasm are normal. × 2,000.

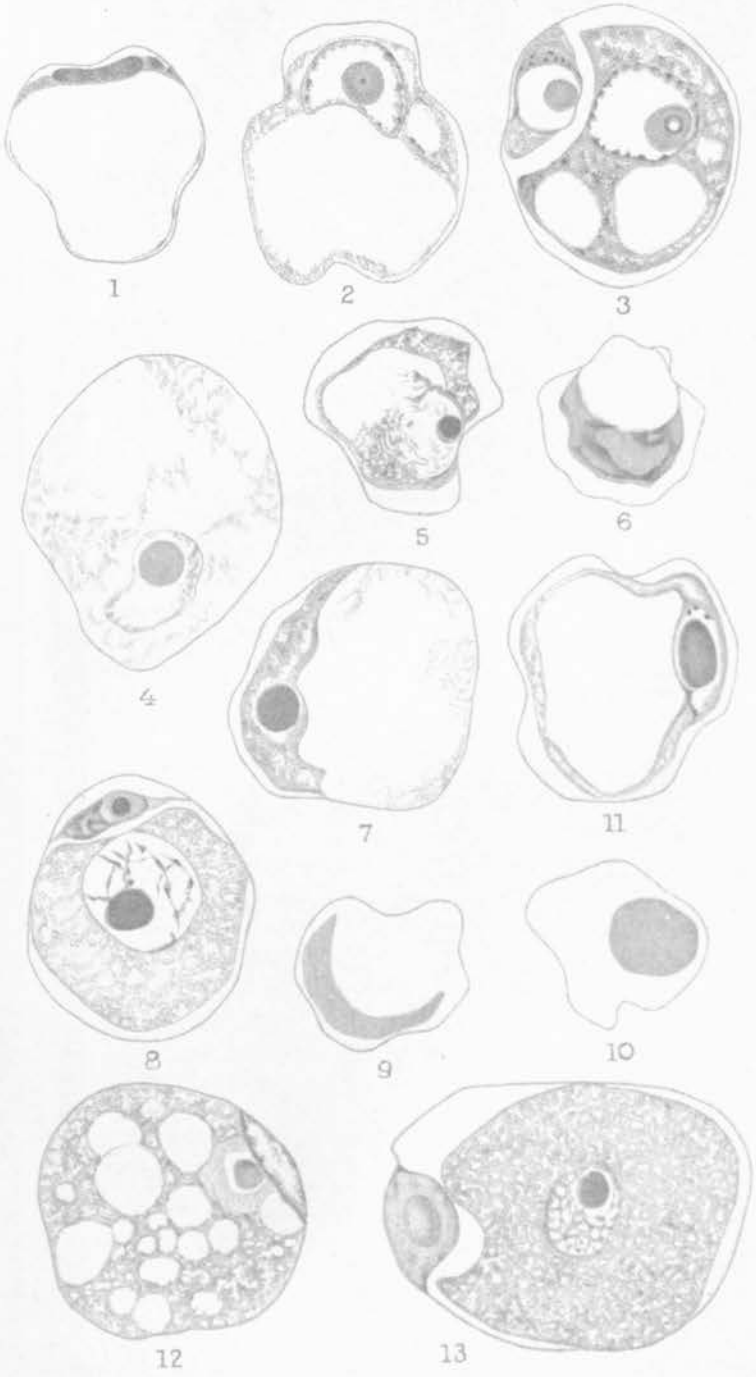

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PLATE 35

A.—Tertiary flower of the pistillate variety, Minnesota 1017×Progressive—13-40, showing prominent staminodia.

B, C.—Primary and secondary flowers of the perfect variety, Minnesota 1017×Progressive—9-24; B showing intermediate and C perfect anthers.

D, E, F.—Two primary and a secondary flower of the perfect variety, Minnesota 1017×Progressive—2-55, showing pistillate, intermediate, and perfect types of flowers.

G, H, I, J.—Flowers from the perfect variety, Minnesota 1017×Progressive—32-1. G and H are primary and secondary flowers, respectively, and are pistillate; I a secondary imperfect flower with a few normally developed stamens and J a tertiary perfect flower.


A
B
C
D
E
F
G
H
I
J

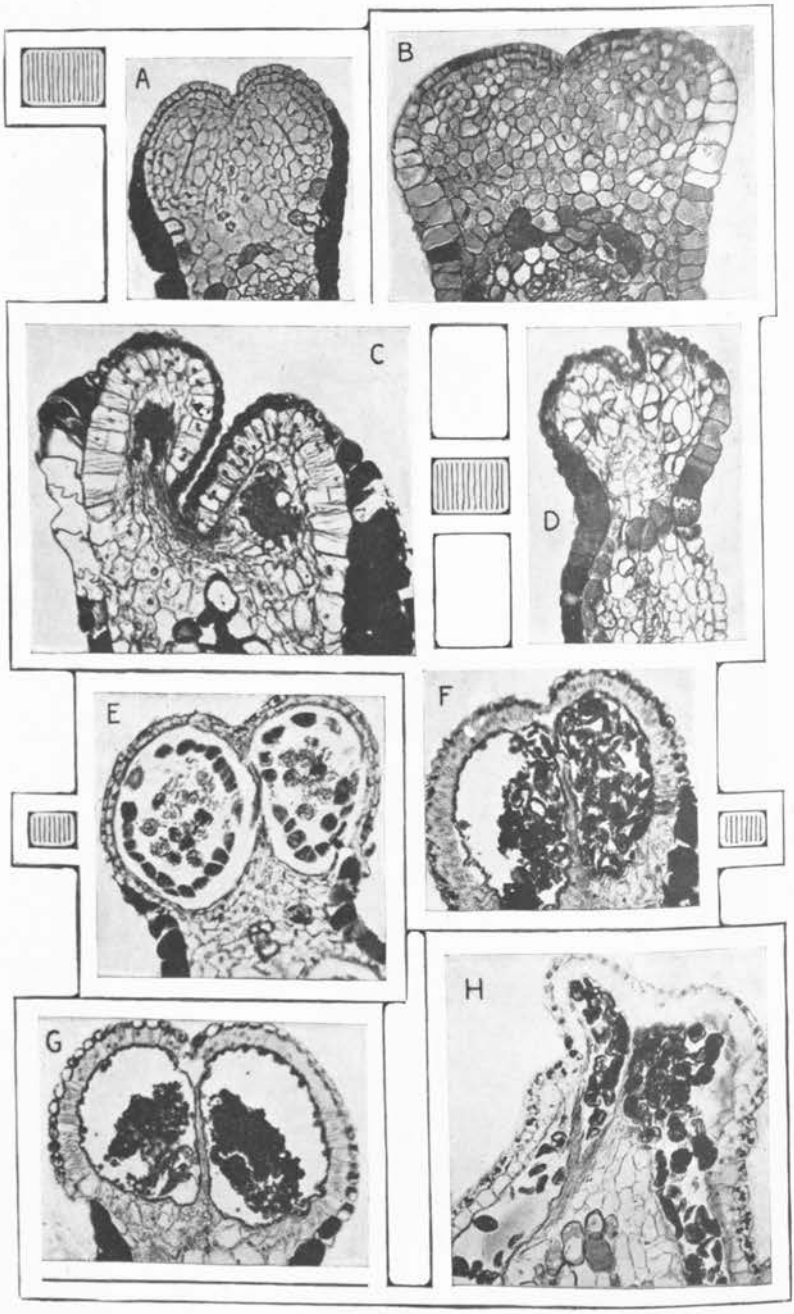
A
B
C
D
E
F
G
H

PLATE 36

A, B, C, D.—Cross sections of two loculi of staminodia of the pistillate varieties, Crescent, Columbia, Minnesota 1017×Progressive—11-59, and Seedling 140, respectively.

E.—Degeneration of the tetrads in an intermediate anther of *Fragaria virginiana*.

F, G.—Later stages of the condition shown in figure E.

H.—A portion of an intermediate anther from the first flower of Minnesota 3.